ANNALS

OF THE

MISSOURI BOTANICAL GARDEN

36

Annals
of the
Missouri Botanical Garden

Volume XXXVI
1949

With 41 plates, and 81 figures

Published quarterly at Galesburg, Illinois, by the Board of Trustees of the Missouri Botanical Garden, St. Louis, Mo.

Entered as second-class matter at the post-office at Galesburg, Illinois, under the Act of March 3, 1879.

Annals

of the

Missouri Botanical Garden

A Quarterly Journal containing Scientific Contributions from the Missouri Botanical Garden and the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

Information

The ANNALS OF THE MISSOURI BOTANICAL GARDEN appears four times during the calendar year: February, May, September, and November. Four numbers constitute a volume.

Subscription Price	$10.00 per volume
Single Numbers	2.50 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

MISSOURI BOTANICAL
RECEIVED
GARDEN LIBRARY

STAFF
OF THE MISSOURI BOTANICAL GARDEN

Director
GEORGE T. MOORE

HERMANN VON SCHRENK,
Pathologist

JESSE M. GREENMAN,
Curator Emeritus of the Herbarium

CARROLL W. DODGE,
Mycologist

EDGAR ANDERSON,
Geneticist

ROBERT E. WOODSON, JR.
Curator of the Herbarium

HENRY N. ANDREWS,
Paleobotanist

ROBERT W. SCHERY,
Research Associate

GUSTAV A. L. MEHLQUIST,
Research Horticulturist

ROLLA M. TRYON,
Assistant Curator of the Herbarium

GEORGE B. VAN SCHAACK,
Honorary Curator of Grasses

JULIAN A. STEYERMARK,
Honorary Research Associate

NELL C. HORNER,
Librarian and Editor of Publications

GERALD ULRICI,
Business Manager

BOARD OF TRUSTEES
OF THE MISSOURI BOTANICAL GARDEN

President
RICHARD J. LOCKWOOD

Vice-President
DANIEL K. CATLIN

Second Vice-President
EUGENE PETTUS

L. RAY CARTER
DUDLEY FRENCH
HENRY HITCHCOCK
JOHN S. LEHMANN
GEORGE T. MOORE
A. WESSEL SHAPLEIGH
ETHAN A. H. SHEPLEY

***EX-OFFICIO* MEMBERS**

ARTHUR H. COMPTON,
Chancellor of Washington University

JOSEPH M. DARST,
Mayor of the City of St. Louis

WILLIAM P. GRUNER,
President of the Academy of Science of St. Louis

WILLIAM SCARLETT,
Bishop of the Diocese of Missouri

HERBERT O. WINTERER
President of the Board of Education of St. Louis

GERALD ULRICI, *Secretary*

vol 36

TABLE OF CONTENTS

		PAGE
Flora of Panama. Part III, Fascicle 4 (Orchidaceae, third part)	Robert E. Woodson, Jr., Robert W. Schery and collaborators	1–132
Flora of Panama. Part III, Fascicle 5 (Orchidaceae, fourth part)	Robert E. Woodson, Jr., Robert W. Schery and collaborators	133–245
Index to Part III of Flora of Panama		247–257
Evidence excluding Mutations, Polysomy, and Polyploidy as Possible Causes of Non-Mendelian Segregations in *Saccharomyces*	Balaji D. Mundkur	259–280
New Species of *Lonchocarpus* from Panama	Frederick J. Hermann	281–284
A First Record for the Genus *Qualea* (Vochysiaceae) from North America (Panama)	Robert W. Schery	285–286
Some Pteridosperm Stems and Fructifications with Particular Reference to the Medullosae	Robert W. Baxter	287–352
Maize Among the Hill Peoples of Assam	C. R. Stonor and Edgar Anderson	355–404
On Some Uses of Maize in the Sierra of Ancash	Charles M. Rick and Edgar Anderson	405–412
Spores of the Genus *Selaginella* in North America North of Mexico	Alice F. Tryon	413–431
The Cytology of *Paphiopedilum Maudiae* Hort.	Henry A. McQuade	433–472
Stegnosperma: A New Species and a Generic Commentary	David J. Rogers	475–477
Nucellangium, A New Genus of Fossil Seeds Previously Assigned to *Lepidocarpon*	Henry N. Andrews, Jr.	479–504
A Revision of the Genus *Heliocarpus*	Ko Ko Lay	507–541
New Apocynaceae of South America	David de Azumbuja and Robert E. Woodson, Jr.	543–548
General Index to Volume XXXVI		551–554

FLORA OF PANAMA

BY

ROBERT E. WOODSON, JR.

AND

ROBERT W. SCHERY

AND COLLABORATORS

PART III

JUNCACEAE–ORCHIDACEAE

From ANNALS OF THE MISSOURI BOTANICAL GARDEN

Vols. XXXII–XXXVI — 1945–1949

CONTENTS

Juncaceae 1

Liliaceae 2

Smilacaceae (Morton) 6

Haemadoraceae 11

Amaryllidaceae 12

Bomarea (Killip) 14

Velloziaceae 25

Dioscoreaceae (Morton) 26

Iridaceae 34

Burmanniaceae (Jonker) 42

Musaceae 48

Zingiberaceae 57

Cannaceae 74

Marantaceae 81

Orchidaceae (Williams) 107

Orchidaceae (Allen) 337

Index 583

SHELVE IN STACKS

Volume XXXVI Number 1

Annals
of the
Missouri Botanical Garden

WASHINGTON UNIVERSITY
MAR 21 1949
MEDICAL LIBRARY

FEBRUARY, 1949

Flora of Panama. Part III. Fascicle 4 (Orchidaceae, third part) . . . .
. Robert E. Woodson, Jr., Robert W. Schery and Collaborators 1–132

PUBLISHED QUARTERLY AT GALESBURG, ILLINOIS,
BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN,
ST. LOUIS, MISSOURI.

Entered as second-class matter at the post-office at Galesburg, Illinois,
under the Act of March 3, 1879.

Annals
of the
Missouri Botanical Garden

A Quarterly Journal containing Scientific Contributions from the Missouri Botanical Garden and the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

Information

The ANNALS OF THE MISSOURI BOTANICAL GARDEN appears four times during the calendar year: February, May, September, and November. Four numbers constitute a volume.

Subscription Price ..... $10.00 per volume
Single Numbers ..... 2.50 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

FLORA OF PANAMA

Part III. Fascicle 4

ORCHIDACEAE[1]

By PAUL H. ALLEN

39. CALANTHE R. Br.

CALANTHE R. Br. in Bot. Reg. 7: sub *t. 573.* 1821; Lindl. Gen. & Spec. Orch. Pl. 249. 1833; Benth. & Hook. Gen. Pl. 3:520. 1883.

Ghiesbreghtia A. Rich. & Gal. Ann. Sci. Nat. III, 3:28. 1845.

Erect terrestrial, or rarely epiphytic herbs, with leafy or sometimes pseudobulbous stems. Leaves few, broadly plicate, with prominent veins. In some of the Old World species the sheathing bases of the leaves envelop the angulate pseudobulbs, the leaf blades becoming deciduous at the end of the season's growth, while in other species the leaves persist for more than one year, with the pseudobulbs much reduced in size or entirely absent. In the single species known to occur in Panama, the two broadly plicate leaves are contracted below into a sheathing petiole arising directly from the rhizome and without any enclosed pseudobulb. Inflorescences erect, many-flowered racemes, equaling or exceeding the leaves in length, the basal portions enveloped by the sheathing leaf bases. Flowers small, on slender pedicels, subtended by linear bracts. Sepals free, subequal, spreading. Petals similar to the sepals or smaller. Lip 3-lobed, prolonged at the base into a spur, the claw of the lip connate to the column. Column short, erect, broadly winged at the apex, the base without a foot. Anther subterminal, operculate, incumbent, 2-celled; pollinia 8, waxy, elongate-pyriform, in groups of 4 in each cell of the anther.

A large genus of the Old World tropics, widely distributed in Africa, Asia and Oceania, with a single species in Central America and the West Indies.

[1]It is particularly desired to acknowledge the cooperation of Professor Oakes Ames of the Botanical Museum of Harvard University in affording the writer the unrestricted use of the Ames Orchid Herbarium and Library. The excellent illustrations by Mrs. Blanche Ames and by Mr. Gordon W. Dillon, used throughout the text, would not have been available without Professor Ames' permission. It is also desired to mention the active cooperation of Dr. Louis O. Williams in providing prompt determinations during the long period of field work in Panama, and, more recently, the very generous help of Mr. Charles Schweinfurth in the solving of many of the critical problems in the course of the preparation of the manuscript.

Issued March 21, 1949.

Fig. 148. *Calanthe mexicana*

1. CALANTHE MEXICANA Rchb. f. in Linnaea 18:406. 1844; Xenia Orch. 1:205, *t. 79, figs. 1–3.* 1856.

Ghiesbreghtia calanthoides A. Rich. & Gal. in Ann. Sci. Nat. III, 3:28. 1845.
Ghiesbreghtia mexicana A. Rich. & Gal. ex Rchb. f. Xenia Orch. 1:205. 1856, in synon.

Erect terrestrial herbs, 25–70 cm. tall. Leaves 2, broadly oblong-elliptic, acute, rather thinly plicate, 30–70 cm. long and 3–14 cm. broad, contracted at the base into a sheathing petiole, arising directly from the rhizome, the basal portions enclosed in 2–3 thin leafless bracts. Inflorescence an erect raceme equaling or exceeding the leaves in length, produced from between the sheathing leaf bases. Flowers few to many, small, white, pedicellate, subtended by linear acuminate bracts 8–20 mm. long and 1–2 mm. broad. Sepals white, free, subequal, spreading, ovate, acute, 7–10 mm. long and 3–6 mm. broad. Petals white, free, spreading, obovate-lanceolate, obtuse, 5–6 mm. long and 2–3 mm. wide. Lip 3-lobed, 8–10 mm. long, prolonged at the base into a spur; lateral lobes erect, minutely puberulent, the upper margins parallel with the column; frontal lobe spreading, yellow, minutely puberulent, subrotund, shortly apiculate, 3–4 mm. long. Ovary puberulent. Capsule ellipsoidal, 2.5–3 cm. long and 1–2 cm. wide.[1]

Mexico, Guatemala, Costa Rica, Panama, and the West Indies.

CHIRIQUÍ: Upper Río Chiriquí Viejo, about 5000–6000 ft., *Seibert 171;* vic. Casita Alta, Volcán de Chiriquí, 1500–2000 m., *Woodson, Allen & Seibert 825;* Finca Lérida to Peña Blanca, 1750–2000 m., *Woodson & Schery 303;* ridges south of Finca Lérida to Loma Sardina, 6000–7000 ft., *Allen 4758;* rain forest, Volcán de Chiriquí, 8000 ft., *Davidson 934;* Bajo Chorro, 7500 ft., *Davidson 203;* Cerro Punta, 2000–2500 m., *Allen & Fairchild 3517.*

A frequent and attractive terrestrial species in the bamboo-oak zone of the upper slopes of Chiriquí Volcano.

40. BLETIA Ruiz & Pavon

BLETIA Ruiz & Pavon, Fl. Peruv. & Chil. Prodr. 119, *t. 26.* 1794; Benth. & Hook. Gen. Pl. 3:513. 1883.

Gyas Salisb. in Trans. Hort. Soc. Lond. 1:299. 1812.
Bletiana Raf. in Amer. Monthly Mag. 4^2:268. 1818, nomen.
Thiebautia Colla, Hort. Ripul. 139. 1824.
Jimensia Raf. Fl. Tellur. 4:38. 1836.
Regnellia Barb. Rodr. Gen. et Spec. Orch. Nov. 1:81. 1877.
Bletilla Rchb. f. in Fl. des Serres 8:246. 1853.

Erect terrestrial herbs, with a few long, lanceolate, plicate, ultimately deciduous leaves which are contracted at the base into a sheathing petiole arising from the apex of a subglobose or sometimes more or less flattened, corm-like pseudobulb considerably resembling that of a Gladiolus. Inflorescences slender, erect, leafless scapes, equaling or exceeding the leaves in length, the basal portion either pro-

[1] Since all measurements have been taken from dried material, it is to be expected that fresh flowers will exceed these figures by at least a third.

duced from the sides of the corm or enveloped in the sheathing leaf bases, the upper portion racemose or sometimes paniculate. Flowers of moderate size or small. Sepals free, subequal, spreading. Petals subequal to the sepals but usually broader. Lip entire or 3-lobed; the lateral lobes broad, usually rounded, erect, in natural position parallel to the column, or sometimes with lobulate, spreading apices; mid-lobe of the lip spreading, with or without an isthmus, the apex often crisped and reflexed, retuse or 2-lobed; the disk with 5–7 more or less fleshy, longitudinal crests or keels. Column elongate, semi-terete, arcuate, the apex winged and the base auriculate. Anther operculate, incumbent, 2-celled; pollinia 8, waxy, flattened, obovate or roughly triangular in outline.

A seemingly natural but perplexing genus in need of revision, now embracing about 50 species distributed from Florida and the West Indies to Mexico and Central and South America as far as Argentina, with three or four species described from the Old World tropics. It seems probable that careful comparison of available material would reduce this list to about a dozen valid species, some of which evidently are widely distributed.

a. Inflorescence enveloped by the sheathing leaf bases. Flowers about 3 cm. long, produced during the rainy season (summer). Highland species..... 2. B. REFLEXA
aa. Inflorescence not enveloped by the sheathing leaf bases. Flowers about 1.5 cm. long, produced during the dry season (winter). Lowland species..... 1. B. PURPUREA

1. BLETIA PURPUREA (Lam.) DC. in Mem. Soc. Phys. Hist. Nat. Genève 9:97, 100. 1841; Huit. Not. Pl. Rar. 23. 1841.

Limodorum purpureum Lam. Encycl. Meth. Bot. 3:515. 1791.
Limodorum verecundum Salisb. Prodr. Stirp. 9. 1796.
Bletia verecunda R. Br. in Ait. Hort. Kew. ed. 2, 5:206. 1813.
Bletia pallida Loddiges, Bot. Cab. 7: *t.* 629. 1822.

Erect terrestrial herbs with 1–4 lanceolate, acuminate, ultimately deciduous leaves 30–70 cm. long and 0.6–4.8 cm. wide, which are contracted below into a sheathing petiole arising from a subglobose or flattened corm-like pseudobulb 2.5–3 cm. in diameter. Inflorescence a slender, erect raceme or panicle, the degree of development depending on the strength of the individual plant, the scape produced from the side of the corm and equaling or exceeding the leaves in length, sometimes flowering after the leaves have fallen. Flowers few to many, rosy purple. Sepals free, subequal, spreading, 1.6–1.8 cm. long and .6–.7 cm. wide, the dorsal sepal ovate-lanceolate, acute, the laterals somewhat oblique at the base, ovate, acute. Petals subequal to the sepals, 1.5–1.7 cm. long and .6–.7 cm. broad, obovate, acute. Lip 3-lobed, about equaling the petals in length, the lateral lobes erect and paralleling the column in natural position, the frontal lobe extended, spreading, more or less crisped and reflexed, the apex bilobed, the inner lip with 7 erect, yellow, parallel, longitudinal, fleshy keels, only 5 of which extend to the frontal lobe. Column slender, arcuate, the apex winged, the base auriculate.

Fig. 149. *Bletia purpurea*

Mexico, Guatemala, British Honduras, Honduras, Costa Rica, Panama, Colombia, Venezuela, and the West Indies.

PANAMÁ: foothills east of Panama City, sea level, *Powell 45;* vic. San Carlos, on walls of river canyons, 0–10 m., *Allen 1149;* along Río Tecúmen, north of Chepo road, about 30 m., *Hunter & Allen 214;* Perlas Archipelago, San José Island, sea cliffs at East Bay, *Johnston 567;* Icaco Island, top of large rocks near coast, *Johnston 922.* COCLÉ: El Valle, banks of Río Antón, 600 m., *Allen 2766;* Río Mata Ahogado, region southeast of El Valle, 200 m., *Allen 3820;* vic. El Valle, *White & White 69.*

A very common and attractive species of the lowlands of the dry Pacific slope, where it is found from sea level to about 3000 ft. elevation, being frequently seen on the nearly vertical walls of the river canyons and in rocky places. The relatively small but brightly colored flowers are produced during the dry season (winter) after the corms have matured and usually after the leaves have fallen.

2. BLETIA REFLEXA Lindl. in Bot. Reg. 21: *t. 1760.* 1835.[1]

Limodorum Lankesteri Ames & Schweinf. in Sched. Orch. 10:78. 1930.
Bletia Lankesteri Ames, Hub. & Schweinf. in Bot. Mus. Leaf. Harv. Univ. 3:41. 1934.

Erect terrestrial herbs with 2–3, usually linear-lanceolate, acuminate, plicate, strongly veined leaves which are ultimately deciduous. Leaves 25–60 cm. long and 0.8–2.5 cm. wide, the basal portions contracted into a sheathing petiole enveloped in 2–3 short, tubular, leafless bracts which are produced from the apex of a short, subconic, corm-like pseudobulb averaging about 1.5 cm. in diameter. Inflorescences erect, the basal portions enclosed in the sheathing leaf bases, the terminal portion an unbranched raceme equaling or exceeding the leaves in length. Flowers relatively large and conspicuous, in our specimens described as being purplish rose, produced on slender pedicels subtended by ovate, acuminate bracts. Sepals free, spreading, subequal, lanceolate, acute, 3–3.2 cm. long and .7–.9 cm. wide, the dorsal usually somewhat narrower. Petals subequal to the dorsal sepal, oblanceolate, acute, 3–3.5 cm. long and about .7 cm. wide. Lip 3-lobed, about 3 cm. long and 2–2.2 cm. wide when spread out, the lateral lobes rounded, erect in natural position, the mid-lobe entire, obtuse, spreading, about 8 mm. long and 8 mm. wide. Inner lip (disk) with 5 fleshy longitudinal crests. Column slender, semi-terete, 2.3–3 cm. long, somewhat dilated at the apex.

Mexico, Guatemala, Costa Rica, and Panama.

CHIRIQUÍ: Llanos del Volcán, 1120–1200 m., *Seibert 328.*

[1] It seems possible that this species may be that originally described as *Bletia campanulata* Llave & Lex. (in Nov. Veg. Descr. Fasc. 2:17. 1825), but the description as given is obscure, and seemingly the type no longer exists. The present material shows rather marked differences from the 'Botanical Register' plate of *Bletia reflexa,* particularly in the shorter central lobe. However, since *Bletia Lankesteri* is about intermediate in this character between our specimens and the typical *Bletia reflexa,* it seems likely that both represent local forms of a widely distributed, somewhat polymorphic species.

41. CHYSIS Lindl.

CHYSIS Lindl. in Bot. Reg. 23: *t. 1937*. 1837; Benth. & Hook. Gen. Pl. 3:514. 1883.

Thorvaldsenia Liebm. in Bot. Not. 103. 1844.

Epiphytic herbs with fleshy, fusiform or clavate, often more or less pendent, pseudobulbous stems. Leaves broadly plicate, the sheathing bases enveloping the pseudobulbs, the leaf blades becoming deciduous at the end of the current season's growth. Inflorescences usually solitary, produced from the axils of one of the lower bracts of the flush of leafy new growth, the scape terminating above in a short, few-flowered raceme. Flowers relatively large and conspicuous. Sepals subequal, free, spreading, the dorsal sepal erect, the broader lateral sepals oblique and adnate to the foot of the column. Petals free, subequal to the sepals, but usually narrower. Lip fleshy, 3-lobed, the lateral lobes rounded or falcate, erect in natural position, or converging over the column, the mid-lobe erect or reflexed, often more or less 2-lobed or emarginate; disk with 3 to 5 longitudinal fleshy crests. Column short, erect, arcuate, broadly winged or roughly triangular in cross-section, produced at the base into a foot. Anther subrotund, operculate, incumbent; pollinia 8, waxy, oblong-ovoid, 4 in each cell of the anther.

Examination of available material in the Ames Herbarium and the Herbarium of the Missouri Botanical Garden would indicate that the genus is probably limited to two somewhat variable species differing fundamentally in the number of fleshy crests of the disk and in the frontal margin of the mid-lobe of the lip. The known geographic range is from Mexico to Peru and Venezuela. A small-flowered, richly colored variety of one of these species is known in Panama from a single collection of flowering material made by Mr. C. W. Powell. Although a few subsequent, sterile specimens have been seen in the field by the writer, it is to be considered as one of the local rarities.

1. CHYSIS AUREA Lindl. var. MACULATA Hook. in Bot. Mag. *t. 4576*. 1851.

Epiphytic herbs, with fleshy cylindric, fusiform or clavate, pendent pseudobulbs 15–20 cm. long and 1–2 cm. wide. Leaves plicate, lanceolate, acute or acuminate, 6–40 cm. long and 1.2–3.5 cm. wide, the imbricating bases persistent, enclosing the pseudobulbs, the blades ultimately deciduous. Inflorescences usually solitary, short racemes produced from the axils of one of the bracts of the leafy new growth. Flowers 3–7, 2.5–3 cm. long in dried specimens but probably somewhat larger when fresh. Dorsal sepal free, erect, elliptic-oblong, obtuse, 2–2.2 cm. long and 1.2–1.5 cm. wide, lateral sepals obliquely cuneate, 2.2–2.5 cm. long and 1.6–1.8 cm. broad, connate at the base and adnate to the column foot, form-

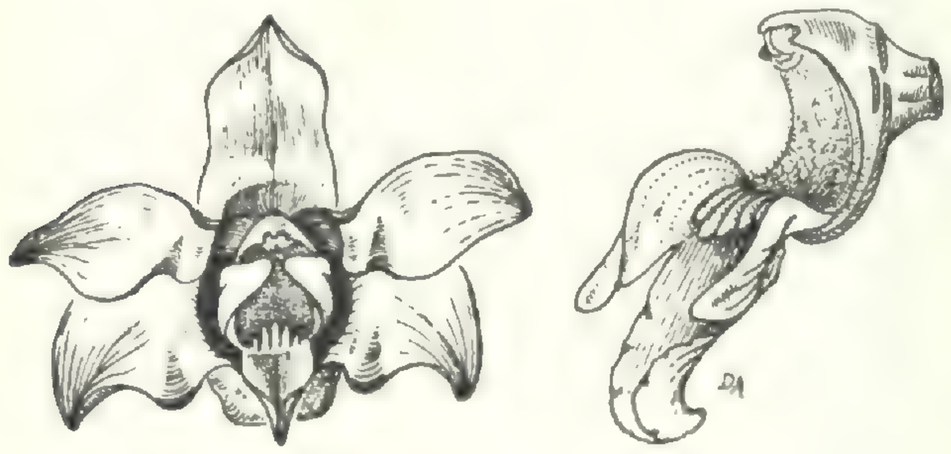


Fig. 150. *Chysis aurea* var. *maculata*

ing a rounded mentum. Petals obovate-lanceolate, acute, 2–2.2 cm. long and 0.9–1.1 cm. broad. Lip 3-lobed, the lateral lobes subfalcate, obtuse, erect, the apices somewhat convergent, the mid-lobe rounded in general outline, more or less cymbiform, the apex 2-lobed or emarginate; disk with 5 fleshy, longitudinal crests. Column short, stout, broadly winged, 0.9–1.0 cm. long and 0.9–1.0 cm. broad at the base, which is produced into a foot.

Costa Rica, Panama, and Colombia.

PANAMÁ: near Arraiján, west of the Canal, about sea level, *Powell 309*.

Chysis aurea var. *maculata* differs from the type in the smaller, more richly colored flowers. The sepals and petals are described as tan, often shaded purple. Lip yellow, the mid-lobe purple, with paler markings.

42. BULBOPHYLLUM Thou.

Bulbophyllum du Petit-Thouars, Hist. Pl. Orch. Iles Aust. d'Afr., Tabl. des Espèc. III, *t. 93–110*. 1822; Benth. & Hook. Gen. Pl. 3:501. 1883.

Didactyle Lindl. in Fol. Orch. 1:57. 1852.
Bolbophyllaria Rchb. f. in Bot. Zeit. 10:934. 1852.

Epiphytic herbs, with short, subconic or angulate, 1- to 2-leaved pseudobulbs often widely spaced along a creeping rhizome. Inflorescences erect or arching spikes or racemes produced from the base of the pseudobulbs. Flowers numerous, inconspicuous, subtended by a bract, free on short pedicels or sessile in shallow pits on the fleshy peduncle. Sepals free, or the laterals connate and obliquely dilated at the base, adnate to the foot of the column. Petals smaller than the sepals, with entire or ciliate margins. Lip simple, fleshy, or with a thickened basal callus, contracted at the base and hinged to the column foot. Column short, erect, produced at the base into a foot. Anther terminal, operculate, incumbent, depressed-hemispherical or obtusely conical, usually 2 celled; pollinia normally 4, waxy, in pairs in the cells of the anther.

There is an extensive list of additional generic synonyms which are not cited because they apply to Old World members of the genus. Since nearly the entire genus is of Old World tropical distribution, where it attains a polymorphic development similar to that of *Epidendrum* in the Americas, it seems futile to attempt a generic description here which will cover the maximum possible limits of floral and vegetative structure. The few species found in the American tropics bear little resemblance to their Old World relatives, and might, for all practical purposes, be separated; but in this case, as in many others, it seems best to follow established usage. The description as given here is intended only to cover the two Panama species, which are identical in superficial appearance, but differ markedly in the size and shape of the petals, and to a lesser extent in the size and form of the lip.

a. Petals acuminate to aristate, exceeding the length of the column; nearly equaling the sepals..... 1. B. ARISTATUM
aa. Petals obtuse, scarcely equaling the length of the column, less than half the length of the sepals..... 2. B. PACHYRRHACHIS

1. BULBOPHYLLUM ARISTATUM (Rchb. f.) Hemsl. Biol. Centr.-Amer. Bot. 3:213. 1883.

Bolbophyllaria aristata Rchb. f. Beitr. Orch. Centr.-Amer. 60. 1861.

Epiphytic herbs 10–35 cm. tall, with short, subpyramidal, angulate pseudobulbs 2.5–5 cm. long and 1–2 cm. wide, usually spaced at intervals along the creeping rhizome. Leaves 2, linear-lanceolate, acute, coriaceous, 6–25 cm. long and 1.5–3 cm. wide. Inflorescences erect racemes 10–40 cm. tall, from the base of the pseudobulbs. Flowers inconspicuous, nearly sessile, subtended by a bract which nearly equals the flower in length. Dorsal sepal free, concave, ovate, acuminate, papillose on the outer surface, 5–6 mm. long and 1.5–2 mm. wide, lateral sepals ovate, acuminate, papillose on the outer surfaces, 4–5 mm. long and 1.5–2 mm. broad, connate at the base and adnate to the foot of the column. Petals lanceolate, acuminate to aristate, 4–7 mm. long and 1.5–3 mm. wide. Lip very fleshy, entire, obtuse, linguiform, 2 mm. long and 1–1.5 mm. wide, hinged to the column foot. Column very short, 1.5–2 mm. long, with two apical, lateral, denticulate processes, the base produced into a foot.

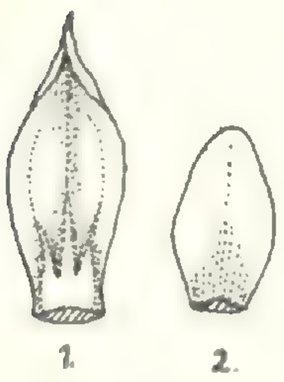


Fig. 151. *Bulbophyllum* petals: 1, of *B. aristatum*, 2, of *B. pachyrrhachis*

Mexico, Guatemala, Honduras, Costa Rica, and Panama.

PANAMÁ: foothills east of city, sea level, *Powell s. n.*; San Juan Range, sea level, *Powell 3492*. COCLÉ: south rim of El Valle de Antón, 650 m., *Allen 2915*; El Valle, lower valley and marshes along Río Antón, about 500 m., *Hunter & Allen 375*. CHIRIQUÍ: Jaramillo, 4500 ft., *Davidson 1270*.

2. BULBOPHYLLUM PACHYRRHACHIS (Rchb. f.) Griseb. Fl. Brit. W. Indies, p. 613. 1864 *(as Bolbophyllum prachyrrhachis)*.

Bolbophyllaria pachyrrhachis Rchb. f. in Walp. Ann. 6:241. 1861.
Bulbophyllum vinosum Schltr. Beih. Bot. Centralbl. 36^2:411. 1918.

Epiphytic herbs 10–45 cm. tall, with short, subconical, strongly 4-angulate pseudobulbs relatively widely spaced along a creeping rhizome. Leaves 2, linear-lanceolate, acute or acuminate, 7–20 cm. long and 0.8–2.4 cm. wide. Inflorescence erect or arching from the base of the pseudobulbs, 10–45 cm. tall, the apical flowering portion of the peduncle often fleshy. Flowers small and inconspicuous, sessile in shallow pits on the peduncle, subtended by broadly triangular bracts. Dorsal sepal free, concave, ovate-acute, 4–5 mm. long and arching over the column, the laterals ovate-acuminate, 4 mm. long and 1.5 mm. broad, connate at the base and adnate to the foot of the column. Petals scarcely equaling the column and less than ⅓ the length of the sepals, oblong-elliptic, obtuse. Lip entire, very

Fig. 152. *Bulbophyllum pachyrrhachis*

fleshy, more or less 3-angled in cross-section, linguiform, the apex obtuse, contracted at the base, and articulated to the column foot.

Mexico, Guatemala, Honduras, Costa Rica, Panama, and the West Indies.

CANAL ZONE: near Frijoles, sea level, *Powell 364;* along Las Cruces trail, between Ft. Clayton and Corozal, *Standley 29102;* foothills east of city, sea level, *Powell s.n.* PANAMÁ: drowned forest of Quebrada Ancha, Madden Lake region, 70 m., *Steyermark & Allen 17104.* VERAGUAS: Río de Jesús, sea level, *Allen 4243.*

43. EULOPHIA R. Br.

EULOPHIA R. Br. in Bot. Reg. 8: *t. 686.* 1823; Benth. & Hook. Gen. Pl. 3:535. 1883.

Cyrtopera Lindl. in Wallich, Numer. List, n. 7362–64. 1832; Gen. & Sp. Orch. Pl. 189. 1833.

Erect, terrestrial herbs with lanceolate, plicate, ultimately deciduous leaves, the basal portions contracted into a sheathing petiole arising from the apex of the short, subconical, tuber-like pseudobulb. Inflorescence an erect, leafless raceme, produced from the base of the tuber-like pseudobulb, equaling or exceeding the leaves. Flowers few to many. Sepals free, subequal, the laterals adnate to the foot of the column. Petals subequal to the sepals, but narrower. Lip 3-lobed, the rounded, lateral lobes erect and converging over the column, the midlobe erect or recurved, sometimes 2-lobed, base of the lip produced into a saccate mentum continuous with the foot of the column. Column short, produced at the base into a foot. Anther terminal, operculate, incumbent. Pollinia 2–4, waxy.

A large genus of mainly Asiatic and African plants represented in Panama by a single species. There seems no point in citing here the extensive list of generic synonyms applicable only to the Old World plants.

1. EULOPHIA ALTA (L.) Fawc. & Rendle, Fl. Jam. 1:112, *t. 22, figs. 4–8.* 1910.

Limodorum altum L. Syst. ed. 12, 2:594. 1767.
Dendrobium longifolium HBK. Nov. Gen. et Sp. 1:360. 1815.
Cyrtopodium Woodfordii Sims, in Bot. Mag. *t. 1814.* 1816.
Cyrtopera Woodfordii Lindley, Gen. & Sp. Orch. Pl. 189. 1833.
Cyrtopera longifolia Rchb. f. in Walp. Ann. 6:668. 1861.
Eulophia Woodfordii Rolfe, in Fl. Trop. Afr. 7:68. 1897.
Eulophia longifolia (HBK.) Schltr. Die Orchideen, p. 347. 1914.

Erect terrestrial herbs with thickened, tuberous rhizomes usually made up of roughly triangular, subconic, corm-like annual sections. Leaves several, erect, lanceolate, acuminate, plicate, strongly veined, ultimately deciduous, 60–120 cm. long and 2–10 cm. wide, contracted below into a cylindric leafy petiole, the broad bases enveloping the corm-like pseudobulb. Inflorescences erect, lateral, leafless scapes, produced from the base of the corm, terminating in a raceme 70–100 cm. tall. Flowers many, of moderate size. Sepals free, erect, subequal, lanceolate to oblanceolate, acute, 2–2.5 cm. long and 0.7–0.8 cm. wide, the laterals adnate at

Fig. 153. *Eulophia alta*

the base to the column foot. Petals erect, oblong, obtuse, subequal to the sepals, 1.5–1.7 cm. long and 0.7–0.8 cm. broad. Lip 3-lobed, lateral lobes rounded, erect, the apices spreading, mid-lobe entire, usually reflexed, with numerous minutely denticulate longitudinal nerves; disk with 2 erect, alate processes, the base subsaccate, forming a rounded mentum with the foot of the column. Column winged, arcuate, 0.8–1.0 cm. long, produced at the base into a foot.

Florida, Mexico, British Honduras, Guatemala, Panama, the West Indies, Colombia, Venezuela, Peru, and Brazil.

PANAMÁ: Mata Redonda, sea level, *Powell 3442;* hills and valleys east of city, sea level, *Powell 10;* vic. La Chorrera, sea level, *Allen 2080.* COCLÉ: vic. El Valle de Antón, 600 m., *Allen 1988.*

Rather frequent terrestrial plants found in areas of wet savanna and along roadways, sometimes persisting in vacant lots in Panama City. The leaves are reminiscent of those of *Bletia* or *Peristeria.* The sepals and petals are green or greenish tan, the lip variously shaded with rose or purple.

43-A. CYRTOPODIUM R. Br.[1]

CYRTOPODIUM R. Br. in Ait. Hort. Kew., ed. 2, 5:216. 1813; Benth. & Hook. Gen. Pl. 3:541. 1883.

Tylochilus Nees in Verh. Bot. Gart. Berlin 8:194, *t. 3.* 1832.

Epiphytic or semi-terrestrial herbs with stout, cylindric or fusiform pseudobulbs. Leaves broadly plicate, strongly veined, more or less distichous, the imbricating bases enclosing the pseudobulb, the blades ultimately deciduous. Inflorescences erect, leafless scapes from the base of the pseudobulbs, racemose or paniculate, equaling or exceeding the leaves. Sepals subequal, free, spreading, the laterals often broader and more or less adnate to the foot of the column. Petals subequal to the sepals but usually broader. Lip 3-lobed, the laterals rounded, erect, parallel with the column or the apices spreading, the mid-lobe entire, retuse or crisped, with a fleshy basal crest, the base adnate to the column foot. Column short, subterete, arcuate, produced at the base into a foot. Anther operculate, imperfectly 2-celled; pollinia 2–4, waxy.

A small genus of American orchids represented in Panama by a single species.

1. CYRTOPODIUM PUNCTATUM (L.) Lindl. Gen. & Spec. Orch. Pl. 188. 1833.

Epidendrum punctatum L. Syst. Nat. 2:1246. 1760.
Cymbidium trinerve Meyer, Prim. Fl. Essequeb. 258. 1818.
Epidendrum gigas Velloso, Fl. Flum. Ic. 9: *t. 20.* 1827.
Cyrtopodium Willmorei Knowles & Westcott, Fl. Cab. 1: *t. 4.* 1837.
Oncidium palmophilum Mart. Herb. ex Lindl. Sert. Orch. sub *t. 12.* 1838.
Cyrtopodium speciosissimum Hort. ex Du Buysson, L' Orchid. 299. 1878.
Cyrtopodium tigrinum Linden, Ill. Hort. 28:95. 1881, nomen tantum.
Cyrtopodium Saintlegerianum Rchb. f. in Flora 68:301. 1885.
Cyrtopodium punctatum var. *Saintlegerianum* Hort. in Stein's Orchideenbuch, p. 181. 1892.

[1] The genus *Cyrtopodium* was unrecorded from Panama when the generic key was written.

Fig. 154. *Cyrtopodium punctatum*

Robust, epiphytic or semi-terrestrial herbs with stout, fusiform pseudobulbs 12–40 cm. long and 2–6 cm. wide, the old pseudobulbs naked or enclosed in the imbricating, persistent leaf bases which are armed at the apex with stout, sharp spines. Leaves linear-lanceolate, acute or acuminate, plicate, distichous, strongly veined, 30–120 cm. long and 2–7.5 cm. wide. Inflorescence a lateral leafless panicle from the base of the pseudobulb, 60–120 cm. tall, the bracts oblong-lanceolate, with undulate margins, resembling the sepals in color and markings. Flowers many. Sepals free, subequal, spreading, oblong-lanceolate, acute or apiculate with strongly undulate margins, greenish yellow spotted irregularly with reddish brown. Dorsal sepal 0.8–2.5 cm. long and 0.8–1.1 cm. wide, lateral sepals 1.5–2 cm. long and 0.7–1.0 cm. wide. Petals free, spreading, obovate, obtuse or apiculate, yellow irregularly spotted red-brown, 1.5–2.0 cm. long and 0.9–1.2 cm. wide. Lip 3-lobed, the lateral lobes erect, more or less convergent over the column, rounded, usually exceeding the mid-lobe in size, reddish-brown shading to yellow at the base, mid-lobe strongly undulant, crisped, yellow, marked purple or reddish brown, crest tuberculate, verrucose, base of lip an oblong limb articulated with the column foot. Column short, arcuate, with a dorsal crest, dilated or semi-auriculate above, narrowed below, produced at the base into a foot.

Florida, Mexico, Guatemala, Costa Rica, the West Indies, Colombia, Venezuela, the Guianas, Brazil, Peru, Paraguay, and Argentina.

PANAMÁ: San José Island, Perlas Archipelago, sea level, *Walker s. n.* (under *Allen 3542*).

Mr. Walker describes the plants as forming colonies on rocks. Although widely distributed in the Americas this is the only known station for the species in Panama.

44. WARREA Lindl.

WARREA Lindl. in Bot. Reg. n. s. 6: Misc. 14. 1843; Benth. & Hook. Gen. Pl. 3:545. 1883.

Erect, terrestrial, highland herbs with lanceolate, acute or acuminate, plicate, strongly veined leaves contracted at the base into a short, stout, sheathing petiole, either with or without an enclosed, short, cylindric, tapering pseudobulb. Inflorescence an erect, leafless raceme produced from the axil of the lowest basal, petiolar bract. Flowers relatively large and conspicuous. Sepals subequal, concave, the bases of the laterals oblique and adnate to the column foot. Petals subequal to the sepals but usually broader. Lip entire, the lateral margins erect; apex spreading, emarginate, 2-lobed, obscurely apiculate or entire; disk lamellate; base of the lip adnate to the column foot. Column elongate, semiterete, with a short basal foot. Anther terminal, operculate, incumbent; pollinia 2 to 4, broadly semiglobose, waxy.

A small, poorly understood genus of American terrestrial orchids at present including about six described species and several varieties ranging from Costa Rica to Colombia, Venezuela, Brazil, and Peru. A single species is known to occur in Panama in the highlands of Chiriquí Province.

1. WARREA COSTARICENSIS Schltr. in Fedde Rep. Sp. Nov. 16:446. 1920.

Erect terrestrial herbs to 70 cm. tall. Leaves 25–60 cm. long and 4–7.5 cm. broad, contracted at the base into a short, stout, sheathing petiole. Inflorescences erect racemes, equaling or slightly exceeding the leaves, produced from the sheathing base of the leafy petiole. Flowers relatively large, reddish bronze, the lip lighter with reddish bronze markings. Dorsal sepal oblong-ovate, obtuse, concave, 3.2–3.5 cm. long and 1.5 cm. broad, lateral sepals subequal to the dorsal sepal, the bases oblique, forming a short rounded mentum with the foot of the column. Petals obovate, obtuse, oblique, 2.8–3 cm. long and 1.3–1.5 cm. wide. Lip entire, 2.5–3 cm. long, and 2.5–3 cm. wide, suborbicular when spread out; basal callus narrow, about 1.5 cm. long. Column slender, arcuate, 2.5 cm. long, produced at the base into a foot.

Costa Rica and Panama.

CHIRIQUÍ: Potrerillos, 3000 ft., *Kieswetter s. n.*; in heavy forest near Potrerillos, *Dunn s. n.*

The present specimens differ from typical material of *Warrea costaricensis* in the entire, not emarginate apex of the lip, and in other minor details. Schlechter's sketch, however, does not seem to agree entirly with his description, which is in some respects nearer to our plant. Since our specimens compare in general quite well with the Costa Rican material it is thought best to consider them as slight geographical variants of an identical species, at least pending more adequate collections upon which to base comparisons.

45. GOVENIA Lindl.

GOVENIA Lindl. in Lodd. Bot. Cab. 18: *t. 1709*. 1831; Benth. & Hook. Gen. Pl. 3:542. 1883.

Eucnemis Lindl. Gen. & Sp. Orch. Pl. 161. 1833.

Erect, terrestrial herbs, with 1 or 2 broadly plicate leaves, the basal portions forming a stout sheathing petiole and enclosing a short, stout, subconical tapering pseudobulb. Inflorescences erect, subcapitate or racemose, equaling or exceeding the leaves, the base enveloped by one of the leafless petiolar bracts. Flowers few to many, of small to medium size, borne on short or elongate pedicels, subtended by short or elongate bracts. Sepals subequal, connivent at the base, the dorsal sepal concave, erect, the laterals more or less falcate or decurved, adnate to the foot of the column, forming a mentum. Petals subequal to the lateral sepals. Lip entire, somewhat concave at the base, spreading, articulated to the foot of the column. Column arcuate, auriculate near the apex, or broadly winged throughout its

length; base produced into a short foot. Anther terminal, operculate, incumbent, 1-celled; pollinia 4, waxy.

A few American terrestrial orchids of remarkably uniform vegetative and floral structure. It seems evident that relatively trivial differences in size, color, length of the raceme, and geographic locality have been considered as adequate for the segregation of most of the so-called species. Only two entities showing any consistent structural differences are known to occur in Panama, where they seem to be confined to the Chiriquí highlands. The sterile plants greatly resemble those of *Calanthe mexicana*.

a. Lip lanceolate, lateral margins minutely ciliate..... 1. G. CILIILABIA
aa. Lip broadly ovate, lateral margins not ciliate..... 2. G. LILIACEA

1. GOVENIA CILIILABIA Ames & Schweinf. in Sched. Orch. 10:80. 1930.

Erect terrestrial herbs 30–36 cm. tall. Leaves 2, broadly plicate, elliptic, shortly acuminate, 30–36 cm. long and 5.5–9 cm. broad, contracted at the base into an elongate sheathing petiole enclosed by 2–3 obtuse or very shortly acute, tubular, imbricating bracts. Inflorescence erect, the sheathing petiole enclosing a slender raceme scarcely equaling the leaves. Flowers small for the genus, membranaceous. Dorsal sepal elliptic-oblong, acute, concave, 10–13 mm. long and 4.2–5 mm. broad, the lateral sepals obliquely elliptic-lanceolate, acute, 9.5–10.5 mm. long and 3.5–3.8 mm. wide. Petals oblique, subfalcate, acute, 10–11 mm. long and 5–5.2 mm. wide. Lip entire, oblong-lanceolate, with minutely ciliate margins; base articulated to the foot of the column. Column arcuate, fleshy, broadly winged, dilated above, 6–7 mm. long, produced at the base into a foot.

Costa Rica and Panama.

CHIRIQUÍ: vic. Casita Alta, Volcán de Chiriquí, 1500–2000 m., *Woodson, Allen & Seibert 947*.

The flowers of the single specimen bear the description: "yellow, purple striped; lip violet rose, with a white tip."

2. GOVENIA LILIACEA Lindl. in Bot. Reg. 21: *t. 1795*. 1836; 24: *t. 13*. 1838.

Govenia utriculata (Sw.) Lindl. in Bot. Reg. 25: Misc. 47. 1839.
Limodorum utriculatum Sw. Prodr. 119. 1788.
Cymbidium utriculatum Sw. in Nova Acta Soc. Sci. Upsal. 6:75. 1799.
Govenia Powellii Schltr. in Fedde Rep. Sp. Nov. 17:51. 1922.

Erect terrestrial herbs 45–65 cm. tall. Leaves 2, plicate, elliptic, shortly acute or lanceolate-acuminate, contracted at the base into a sheathing petiole, the bases enclosing a short, stout, fleshy, cylindric, tapering pseudobulb. Inflorescences erect, leafless scapes, racemose or subcapitate, less than, equal to, or exceeding the leaves, the bases enveloped by the tubular imbricating petiolar bracts. Flowers few to many. Dorsal sepal lanceolate, shortly acuminate, 10–16 mm. long and 4–5 mm. broad, lateral sepals oblique, lanceolate, subfalcate, acute, 8–11 mm. long and 4–5 mm. wide. Petals oblanceolate, acute, 10–11 mm. long and 5–6 mm. wide. Lip entire, broadly ovate, acute, 6–9 mm. long and 4.5–7.5 mm. broad, strongly

nerved, the nerves often branching; base articulated to the column foot. Column short, arcuate, 7–8 mm. long, broadly winged and often subauriculate at the apex, produced at the base into a foot.

Mexico, Guatemala, Salvador, Honduras, Costa Rica, Panama, the West Indies, Venezuela, Brazil, Argentina, and Bolivia.

CHIRIQUÍ: in damp, shady places, 4000 ft., *Powell 205;* valley of the upper Río Gariché, 1050–1100 m., *Seibert 329;* Jaramillo, Boquete, 5000 ft., *Davidson 798;* Casita Alta to Cerro Copete, 2300–3000 m., *Woodson & Schery 345;* Volcán de Chiriquí, 8000 ft., *Davidson 934, 946.*

The last three specimens cited seem to show consistent differences from the rest in the longer racemes, the abundant linear bracts, and in the somewhat smaller flowers. In spite of this, however, no significant structural differences could be detected in the flowers. Under the circumstances it is considered best to include them here, at least until the genus as a whole is critically studied.

46. MORMODES Lindl.

MORMODES Lindl. Introd. Nat. Syst. Bot. ed. 2, 446. 1836; Benth. & Hook. Gen. Pl. 3:552. 1883.

Cyclosia Kl. in Allgem. Gartenzeit. 6:305. 1838.

Epiphytic herbs, with cylindric or fusiform pseudobulbs usually tapering uniformly upward. Leaves plicate, strongly veined, distichous, the unarmed imbricating bases enclosing the pseudobulbs; leaf blades deciduous. Inflorescences arching racemes produced from the base or lower sides of the pseudobulbs. Flowers few or many, often richly colored. Sepals free, subequal, spreading or strongly reflexed. Petals subequal to the sepals or sometimes broader. Lip entire or 3-lobed, often fleshy, the lateral lobes or margins usually strongly reflexed, base often with a claw which is adnate to the base of the column. Column usually curved and twisted to one side so that the dorsal surface of the apex rests against the lip, the anther and stigmatic surface being thus exposed; rostellum without antennae, base of the column without a foot. Anther terminal, operculate, incumbent, 1- or imperfectly 2-celled, extremely sensitive; pollinia 2 or 4, waxy, often ejected during the process of pressing the flowers and found adhering to the lip, or to one of the other floral parts.

An interesting genus of American epiphytic orchids, ranging from Mexico to Peru and Brazil, vegetatively reminiscent of *Catasetum,* but readily distinguishable even when not in flower by the absence of spines on the upper margins of the imbricating leaf bases enveloping the old pseudobulbs. Many species have been described, often founded on single specimens flowering in European greenhouses. Although many entities enter into the present confused picture, it seems probable that most represent color forms of either *Mormodes igneum* or *M. atropurpureum.* In spite of this abundance of named color forms, valid diagnostic characters seem to exist, based mostly on the lobes in the lip, whether present or absent, and their

relative size, shape or indument. Although even these characters are subject to a certain amount of individual interpretation, four fairly well-marked entities can be separated in Panama. Due to the extreme tortion of all of the floral parts, it is generally necessary to spread the lip out fully to obtain any adequate idea of its shape.

a. Lip distinctly 3-lobed, about as long as broad; mid-lobe projecting conspicuously beyond the laterals, the apex sometimes recurved..... 1. M. ATROPURPUREUM
aa. Lip entire, or of two lateral lobules with a shortly apiculate apex.
  b. Blade of lip elliptic-ovate to rhombic-ovate, acute or acuminate, not abruptly apiculate, about twice as long as broad..... 2. M. COLOSSUS
  bb. Blade of lip obovate, oval or suborbicular, obtuse, or truncate, abruptly apiculate, about as long as broad.
    c. Lip glabrous..... 4. M. IGNEUM
    cc. Lip pubescent..... 3. M. HOOKERI

1. MORMODES ATROPURPUREUM Lindl. Introd. Nat. Syst. Bot., ed. 2, 446. 1836, non Hook.

Epiphytic herbs with very stout pseudobulbs. Inflorescences erect racemes, produced from near the base of the pseudobulbs. Sepals subequal, free, spreading, lanceolate, acute or acuminate, the dorsal sepal 2.4–2.6 cm. long and .6–.7 cm. wide, laterals lanceolate, acute or acuminate, 2.6–2.8 cm. long and .7–.8 cm. wide. Petals elliptic-lanceolate, acute, 2.5 cm. long and .9–1.1 cm. wide. Lip distinctly 3-lobed, 1.8–2 cm. long and 1.8–2 cm. wide when spread out, the lateral lobes rounded and strongly reflexed, the entire mid-lobe projecting beyond the laterals, subcuneate, abruptly apiculate. Column twisted to one side. Flowers described as "red-brown, with small spots. Lip rose, spotted with red-brown."

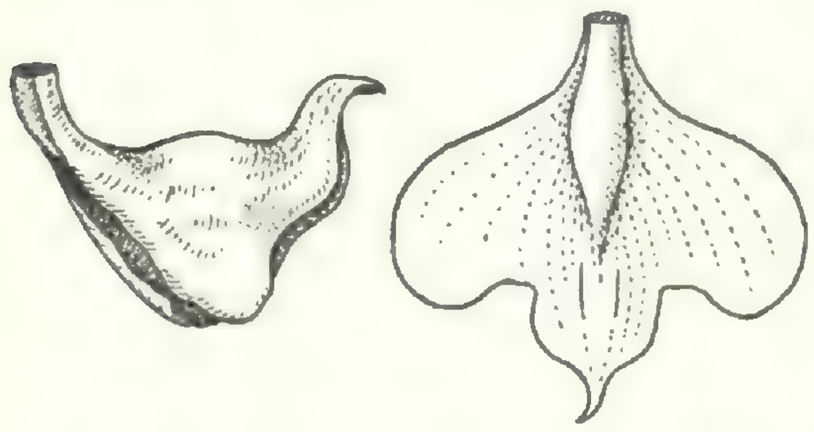


Fig. 155. *Mormodes atropurpureum*—lip

Costa Rica and Panama.

CHIRIQUÍ: Caldera River, 3500 ft., *Powell s. n.*; Concepción, 800 ft., *Powell s. n.*; vic. Progreso, 1000 ft., *Dunn s. n.*

Seemingly rare. Most of the specimens previously determined as *Mormodes atropurpureum* Lindl. are dark red color forms of *M. igneum*.

2. MORMODES COLOSSUS Rchb. f. in Bot. Zeit. 10:636. 1852.

Mormodes macranthum Lindl. & Paxt. in Paxton's Flow. Gard. 3:98. 1852–53.
Mormodes Wendlandii Rchb. f. in Walp. Ann. 6:581. 1861.
Mormodes Powellii Schltr. in Fedde Rep. Sp. Nov. 17:55. 1922.

Epiphytic herbs. Pseudobulbs often long, cylindric, tapering. Leaves plicate, deciduous, the persistent imbricating bases unarmed. Inflorescences long arching racemes produced from near the base of the pseudobulbs. Sepals subequal, spreading, linear-lanceolate, acuminate, 3.5–5 cm. long and .6–.8 cm. wide. Petals subequal to

Fig. 156. *Mormodes colossus*—lip

the sepals, lanceolate, acuminate, 3.2–4.5 cm. long and .7–1.0 cm. wide. Lip elliptic-ovate to rhombic-ovate, acute or acuminate, 3.2–5 cm. long and 1.6–2.5 cm. wide when spread out, the lateral margins often strongly recurved, dried specimens frequently giving the impression of being linear-lanceolate; base shortly clawed. Column 1.5–1.7 cm. long, twisted to one side, typical of the genus.

Costa Rica and Panama.

CANAL ZONE: Gatún Lake and Río Chagres, sea level, *Powell s. n.*; Ana Lago, sea level, *Powell s. n.*; Gatún Lake, *Powell s. n.*; upper Chagres region, *Powell s. n.* COCLÉ: vic. El Valle de Antón, 800–1000 m., *Allen 76;* El Valle, *Cope s. n., Fairchild s. n.*

There seem to be no consistent structural differences upon which to separate *M. macranthum*, *M. Wendlandii* or *M. Powellii* from *M. colossus*. The species is somewhat variable, particularly in the size and coloration of the flowers. They are variously described in Panama as with "Sepals and petals olive green, yellowish brown or cream. Lip brown, tan or yellow. Fragrant." The specimens from El Valle de Antón are smaller than typical *M. colossus*, and the lip rather broader near the base when spread out, but both these differences represent deviations in degree rather than in the presence or absence of any essential character.

3. Mormodes Hookeri Lem. Jard. Fleur. 1: Misc. 116. 1851–54.

Mormodes atro-purpurea Hook. in Bot. Mag. *t. 4577*. 1851, non Lindl.
Mormodes barbatum Lindl. & Paxt. in Paxton's Flow. Gard. 2:57. 1851–53.

Epiphytic herbs; pseudobulbs dwarf, in specimens seen about 8–10 cm. tall, otherwise typical of the genus. Leaves plicate, deciduous. Inflorescences short erect racemes from the base of the pseudobulbs. Flowers few to many, dark reddish brown or red; if many, set closely together in a dense raceme. Sepals subequal, lanceolate, acuminate, strongly reflexed, dorsal sepal 1.8–2 cm. long and .45–.5 cm. wide, laterals 1.7–1.8 cm. long and .55–.65 cm. wide. Petals subequal to the sepals, lanceolate, acuminate, strongly reflexed, 1.6–1.8 cm. long and .55–.65 cm. wide. Lip obovate, truncate, abruptly and minutely apiculate, about as long as broad when spread out, 1.4–1.6 cm. long and 1.4–1.6 cm. wide, lateral lobes very strongly reflexed, pubescent. Column twisted to one side, typical of the genus.

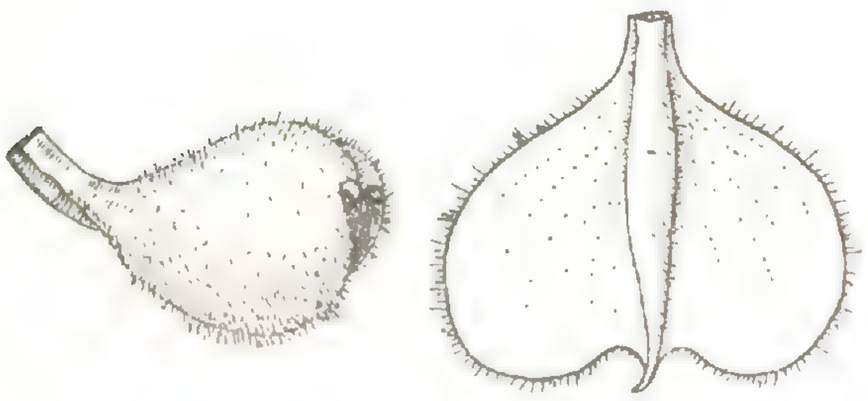


Fig. 157. *Mormodes Hookeri*—lip

Panama and Costa Rica.

Although no herbarium material of this species is at present available from Panama, it appears in the 'Botanical Magazine' (*t. 4577*) under the erroneous name of *Mormodes atro-purpurea* Hook., with the notation that it had been obtained from one of the sales of Warscewicz's Panama plants. Also, a plant was flowered in the Missouri Botanical Garden collection in Balboa, C. Z. in 1940, having been collected in the vicinity of El Valle de Antón, in Coclé Province. Unfortunately these flowers were not preserved. The species is therefore listed without hesitation for our area, in spite of the lack of actual specimens. Schlechter's citation of *M. Hookeri* in Panama may probably be based on specimens in some European herbarium, but actually all specimens seen by the writer which had been determined by Schlechter as such are dark red color forms of *M. igneum*. Except for the pubescent lip and the dwarf habit, the species is not remarkably distinct from *M. buccinator*, and may, in fact, prove to be only a very distinct variety or geographical race.

4. MORMODES IGNEUM Lindl. & Paxt. in Paxton's Flow. Gard. 3:97, *t. 93*. 1852–53.

Epiphytic herbs. Pseudobulbs stout, cylindric, tapering uniformly from the base upward, 10–35 cm. tall and 1–5 cm. wide. Leaves 5–15, plicate, distichous, strongly veined, the persistent, closely imbricating, unarmed bases closely enveloping the pseudobulbs, the lanceolate, acuminate blades deciduous at the end of the growing season. Inflorescences 1 to several, erect, arching racemes produced in succession from near the base of the pseudobulbs. Flowers few to many, variable in color, size, and texture. Sepals subequal, membranaceous, yellow, olive-green, tan-brown or red, often with minute spots, the dorsal sepal erect, lanceolate, acuminate or apiculate, 1.8–2.8 cm. long and .5–.7 cm. wide, the laterals lanceolate, acuminate, strongly reflexed, 1.5–2.7 cm. long and .4–.7 cm. wide. Petals subequal to the sepals, similarly colored, elliptic-lanceolate, acute, usually strongly reflexed, 2–2.5 cm. long and .6–.8 cm. wide. Lip suborbicular when spread out, shortly apiculate, glabrous, usually fleshy to very fleshy, white, yellow, olive-green, tan, brown, or dark reddish brown, often with minute brown or reddish brown spots, the lateral margins strongly reflexed, the base conspicuously clawed. Column twisted to one side, typical of the genus.

Costa Rica, Panama, and Colombia.

CANAL ZONE: Gatún Lake, *Powell s. n.*; Frijoles, *Powell s. n.*; Las Cascadas, *Powell s. n.* PANAMÁ: San Juan, *Powell s. n.*; upper Chagres, *Powell s. n.*; foothills east of city, *Powell s. n.*; Río La Maestra, 0–25 m., *Allen 64*; Cerro Campana, 1000 ft., *Fairchild s. n.* COCLÉ: lower valley and marshes along the Río Antón, El Valle de Antón, 500 m., *Hunter & Allen 388*; hills south of El Valle de Antón, 700 m., *Fairchild s. n.*; floor of El Valle de Antón, 600 m., *Allen 3985, 5182*. VERAGUAS: vic. Santa Fé, 1000 ft., *Allen 4419*. CHIRIQUÍ: 800 ft., *Powell s. n.*; Caldera River, 3500–4000 ft., *Powell s. n.*

WASHINGTON UNIVERSITY LIBRARY MEDICAL SCHOOL

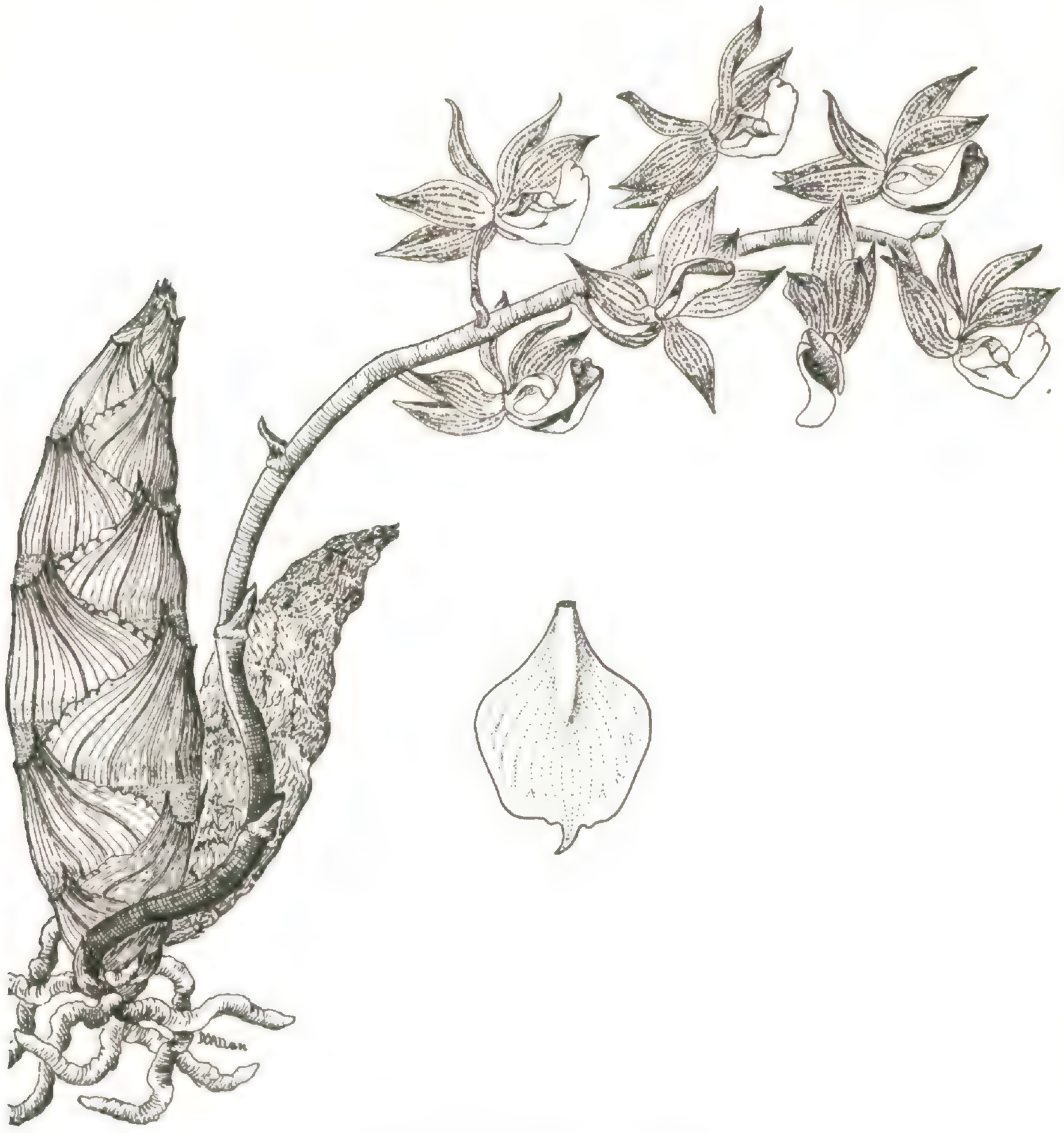


Fig. 158. *Mormodes igneum*

This is by far the most frequent species of *Mormodes* found in Panama, distributed throughout the lowlands of both coasts and ascending to about 4000 feet on the Pacific slope. The plants are frequently found growing in the tops of dead trees or on projecting dead branches, displaying a marked preference for decaying wood and exposure to full sun. The flowers are extremely variable in color and to a lesser degree in size and texture, scarcely any two being exactly alike.

47. CATASETUM L. C. Rich.

CATASETUM L. C. Rich. ex Kunth, Syn. Pl. Aequin. 1:330. 1822; Benth. & Hook. Gen. Pl. 3:551. 1883; Mansfeld, in Fedde Rep. Sp. Nov. 30:257–275. 1932; 31:99–125. 1932.

Myanthus Lindl. in Bot. Reg. 18: sub *t. 1538*. 1832.
Monachanthus Lindl. loc. cit. 1832.
Cuculina Raf. Fl. Tellur. 4:49. 1836.

Monacanthus G. Don. in Sweet, Hort. Brit. 3:644. 1839.
Catachaetum Hoffmsgg. Verz. Orchid. 22. 1842.
Clowesia Lindl. in Bot. Reg. 29: Misc. 25, *t. 39.* 1843.
Warczewitzia Skinner in Lindl. & Paxton's Flow. Gard. 1:45. 1850–51.

Epiphytic herbs. Pseudobulbs fleshy, fusiform, or subconic; roots often with many secondary, slender, erect, spinous rootlets which form dense mats about the base of the plants. Leaves plicate, strongly nerved, the blades deciduous; the persistent imbricating bases closely enveloping the pseudobulbs, armed at the apex with short, sharp spines. Inflorescences arching or pendulous racemes from the base of the pseudobulbs. Flowers few or many, often large and showy, unisexual or perfect. Sepals and petals in all forms free, subequal, fleshy or membranaceous, part or all of them spreading or reflexed and connivent at the base. The genus is divided by Mansfeld into two distinct sections. In CLOWESIA: flowers perfect (containing both a functional stigmatic surface and a fertile anther); column without elongate antenna-like processes; lip membranaceous or fleshy. In ORTHOCATASETUM: flowers unisexual, the staminate and pistillate forms strikingly dissimilar and usually produced on separate scapes; staminate flowers (those most frequently seen) usually many, often conspicuously colored, on an arching or pendent raceme; lip membranaceous, fleshy, spreading, concave or galeate, the margins entire, lobulate, emarginate, crenate, fimbriate or dentate; column erect, footless, the under-side usually with two elongate antenna-like processes which are extremely sensitive when touched, ejecting the pollinia with considerable force. Anther terminal, operculate, incumbent, convex, 1-celled or imperfectly 2-celled; pollinia 4, waxy, in 2 pairs, or 2-lobed or 2-sulcate. Pistillate flowers less frequently produced, usually few, on short, erect or arching racemes. Lip usually very fleshy and galeate, with or without a thickened margin. Column short and stout, without antennae; functional stigmatic surface present.

A large and remarkable genus of American orchids ranging from Mexico to Peru and Brazil. They are among the most interesting of all known orchids, but segregation of the various entities has been delayed and confused by the dimorphism of the flowers. Many synonymous names have been added to the literature from specimens flowering in European greenhouses, most being color forms of now well-known species. However, much remains to be done, and some instances still exist (in the section ORTHOCATASETUM) where only the staminate, or the pistillate form is known, or at least the forms have not been correlated with each other. Both sections of the genus are represented in Panama, each with three species.

a. Flowers perfect. Column without elongate antennae. (Section CLOWESIA.)
  b. Lip 3-lobed, membranaceous, apical lobe fimbriate..... 6. C. WARCZEWITZII
  bb. Lip entire, very fleshy, apex obtuse or acute.
    c. Sepals and petals very strongly reflexed. Apex of the lip acute.... 4. C. SUAVE
    cc. Sepals and petals spreading. Apex of the lip obtuse..... 2. C. EBURNEUM
aa. Flowers dimorphic. Column of the staminate flowers (in the Panama species) with 2 elongate antennae. (Section ORTHOCATASETUM.*)

*The key in this section is based on staminate flowers. It is usually difficult or impossible to identify the pistillate flowers, particularly from dried material.

b. Lip of the staminate flowers with 5 elongate, marginal processes. Total length of the lip 1 cm. or less..... 1. C. BICOLOR

bb. Lip of the staminate flowers without elongate marginal processes. Total length 2 cm. or more.

c. Lip globose above, with an abrupt, conical, basal constriction, lateral margins minutely ciliate; inner lip strongly rugose-striate.... 5. C. VIRIDIFLAVUM

cc. Lip obconic, uniformly tapering, the base not abruptly constricted, lateral margins fimbriate; inner lip glabrous..... 3. C. OERSTEDII

1. CATASETUM BICOLOR Klotzsch, in Allgem. Gartenzeit. 22:337. 1854.

Catasetum gongoroides Kränzl. in Fedde Rep. Sp. Nov. 23:254. 1930.

Epiphytic herbs. Pseudobulbs dwarf, subconic or cylindric, tapering, 4–9.5 cm. long and 2.5–4 cm. wide. Leaves plicate, distichous, elliptic-lanceolate, acute or acuminate, the imbricating persistent bases enveloping the pseudobulbs, the old growth armed at the apex with sharp spines, the leaf blades deciduous at the end of the growing season. Flowers unisexual, dimorphic, produced on separate scapes. Staminate inflorescences arching or pendent racemes 8–15 cm. long, from the base of the pseudobulbs. Sepals subequal, free, lanceolate, acuminate, brownish green, purplish, flesh-pink or dark reddish brown, 2.5–4 cm. long and 2.8–3.2 mm. wide, dorsal sepal erect, laterals strongly reflexed or spreading, often more or less parallel with the elongate peduncle. Petals subequal to the sepals, elliptic-lanceolate, acute, pale green, purplish green, or flesh-pink, spotted red-brown, 2.5–3 cm. long and 4–5 mm. wide, erect and closely approximating the dorsal sepal, the three segments closely arching over the column. Lip short, the base saccate, the apex complexly 3-lobed; lateral lobes erect, 2 on each side, about equaling the saccate base in length, the upper pair linguiform, obtuse, the lower pair linear-lanceolate, acuminate; mid-lobe triangular, spreading, the entire lip including lobes 5–10 mm. long, white or pale yellow, the margins of the central lobe red-brown, the lateral lobes and inner surface of the saccate base also irregularly blotched red-brown. Column slender, erect, conspicuously rostrate at the apex, winged, 12–15 mm. long and about 4 mm. broad, under-surface with 2 elongate antennae, the points of which extend to the inner base of the saccate lip. Pistillate flowers relatively rare, produced on few-flowered, erect racemes 8–10 cm. tall, from the base of the pseudobulbs. Sepals free, subequal, spreading or reflexed, coriaceous, elliptic-lanceolate, acute, pale green, 2 cm. long and 4–6 mm. wide. Petals subequal to the sepals, spreading, coriaceous, elliptic-lanceolate, with oblique acute tips, green, minutely spotted red-brown, 2–2.3 cm. long and .6–.7 cm. wide. Lip fleshy, calceiform, yellowish green, 18–20 mm. long and 15 mm. wide, with an acute, thickened, broadly triangular apex. Column short, stout, broadly triangular in cross-section, 8 mm. long and 7 mm. wide, with a narrow, lunate functional stigmatic surface.

Panama and possibly Colombia.

Fig. 159. *Catasetum bicolor*

CANAL ZONE: Limon Island, vic. Nuevo Limon, Gatún Lake, 80 ft., *Cope & Babbitt s. n.*; Barro Colorado Island, *Zetek s. n.*; without definite locality, *Barrett s. n.* COLÓN: Cerro Santa Rita, 1200 ft., *Allen & Fairchild 5181.* CHIRIQUÍ: Chiriquí Volcano, 3000–3500 ft., *Powell 168.*

Frequent plants of the upper slopes of the wet forested mountains of Colón Province, where they are usually found growing on old logs and stumps, showing a decided preference for dead and decaying wood. Also recorded from the slopes of Chiriquí Volcano, but not seen there in recent years. The plants when not in flower are almost identical in vegetative appearance with those of *Catasetum Warczewitzii.*

2. CATASETUM EBURNEUM Rolfe, in Kew Bull. 86. 1906.[1]

Epiphytic herbs. Pseudobulbs cylindric, tapering, 5–8 cm. tall and 2–2.5 cm. wide. Leaves plicate, with 3 prominent veins, lanceolate, acuminate, 15–30 cm. long and 2–3.5 cm. wide; the persistent imbricating bases enveloping the old pseudobulbs, armed at the apex with sharp spines; the leaf blades ultimately deciduous. Inflorescence an arching raceme from the base of the pseudobulb, 18–30 cm. long. Flowers perfect, waxy white, the lip shaded and spotted yellow, fragrant. Sepals fleshy, subequal, free, spreading, or somewhat reflexed, oblong, obtuse, 1.7–2 cm. long and .8–1 cm. wide. Petals fleshy, spreading, ovate-elliptic, acute, 1.3–2 cm. long and 1–1.2 cm. wide. Lip entire, very fleshy, saccate, adnate to the base of the column, broadly ovate, obtuse; inner lip with two lateral erect ridges on either side of the basal concavity, terminating toward the apex in a low, emarginate, fleshy crest. Column very short, stout, terete, 8 mm. long and 8 mm. broad, without antennae. Anther with obtuse lateral lobules, the apex sagittate.

Panama and Colombia.

PANAMÁ: Cerro Campana, on low trees along margins of grassland, 2500 ft., *Allen 4559.*

A seemingly rare species, thus far known only from a few plants collected on the upper slopes of Cerro Campana where they were found on low trees on the margins of the extensive grasslands. Vegetatively they are reminiscent of immature plants of *C. viridiflavum*, but lack the erect, spinous, matted, secondary rootlets so characteristic of that species.

---

[1] *Catasetum eburneum* is considered by Mansfield to be referable to the earlier *dilectum* Rchb. f. (Beih. Orch. Central-Amer. 73. 1866). However, careful comparison of our material with the Reichenbach description and drawing of the type in the Ames herbarium has disclosed wide discrepancies in nearly every essential structural detail. The description of *eburneum* by Rolfe, on the other hand, agrees with our specimens in almost every respect except that our flowers are somewhat smaller. Since our plant flowered in cultivation under somewhat abnormal conditions, some difference in size would be expected.

Fig. 160. *Catasetum eburneum*

3. CATASETUM OERSTEDII Rchb. f. in Bonplandia 3:218. 1855.

Catasetum rostratum Klinge, in Acta Hort. Petropol. 17:134, *t. 2.* 1898.
Catasetum Brenesii Schltr. Beitr. Orchk. Zentralam. 2:136, 225. 1923.

Stout epiphytic herbs with fusiform pseudobulbs 8–30 cm. tall and 3.5–5 cm. wide; roots with many slender, erect, spinous secondary rootlets, forming a dense mat about the base of the plants. Leaves 5–12, plicate, strongly nerved, elliptic-

lanceolate, acute or acuminate, 15–60 cm. long and 3–12 cm. wide, the blades deciduous at the end of the growing season, the persistent imbricating bases enveloping the old pseudobulbs, armed at the apex with sharp spines. Inflorescences arching racemes 12–50 cm. long, produced from the base of the pseudobulbs. Flowers relatively large and conspicuous, unisexual, dimorphic, the staminate and pistillate forms produced on separate scapes. Staminate flowers those most frequently seen, few to many on an arching raceme. Sepals membranaceous, free, green, greenish brown or marked with purple or red-brown, the dorsal sepal concave, oblanceolate, curving over the column, acuminate, 3.5–4 cm. long and 1.2–1.4 cm. wide, the laterals spreading, more or less oblique, lanceolate, acuminate, 4–4.5 cm. long and 1.5–1.7 cm. wide when spread out, the margins often involute. Petals membranaceous, green or marked with purple or red-brown, elliptic-oblanceolate, obliquely acuminate, 3.5–4 cm. long and 1.8–2 cm. wide, the inner margins somewhat overlapping below the dorsal sepal, forming with it a concave trough under the column. Lip very firm and fleshy, obconic, uniformly tapering, 2.5–3.5 cm. long and 2–2.2 cm. wide, green, marked or spotted purple, red-brown, or yellow, glabrous on the outer surface and within except for a fleshy lunate callus just below the apical margin, lateral margins fimbriate, the apex emarginate or rarely entire. Column rostrate, arcuate, broadly winged, 3 cm. long and 1–1.2 cm. wide, the under-surface with 2 slender elongate antennae, one unciform, closely approximating the base of the column, the other slightly undulate, the tip extending nearly to the innermost base of the lip. Pistillate flowers relatively infrequent, fleshy, green on outer surfaces, yellow within, usually 2–3 on erect racemes, very similar to those of *C. viridiflavum*, but with the lip somewhat shorter, broader, and rounder.

Nicaragua (*fide* Mansfeld), Costa Rica, Panama, and possibly Colombia.

VERAGUAS: vic. Soná, 200 m., *Allen 2664;* vic. San Felix, 100 m., *Allen 3658.* CHIRIQUÍ: near Dolega, 1000 ft., *Powell 351;* vic. Remedios, 100 ft., *Allen 4505, 4506, Allen & Fairchild 3512;* vic. Progreso, 500 ft., *Dunn s. n.;* vic. Concepción, 1000 ft., *Allen 5165.* BOCAS DEL TORO: Chiriquí Lagoon, Bastimentos, *von Wedel 2906;* Water Valley, *von Wedel 638, 863, 1375, 1435;* Western River, *von Wedel 2780;* Little Bocas, *von Wedel 2544;* Isla Colón, Macaw Hills, *von Wedel 523, 555;* Careening Cay, *von Wedel 568.*

A robust, very frequent species of the lowlands of Bocas del Toro, Chiriquí, and Veraguas provinces. It seems to be entirely confined, so far as known, to the western portion of the Republic, being replaced in the vicinity of the Canal by *C. viridiflavum.* The staminate flowers are extremely variable in color, and to a lesser degree in size.

It seems possible that this species may be that collected in 1801 by Humboldt and Bonpland near Cartagena, Colombia, and described by Kunth (Syn. Pl. Aequin. 1:331. 1822) as *Catasetum maculatum.* However, since the description does not agree with the plate in Humboldt, Bonpland and Kunth's 'Nova Genera et Species Plantarum', and since the type apparently no longer exists, it seems best to follow Mansfeld and adopt *C. Oerstedii* as the next available, well authenticated name.

4. CATASETUM SUAVE Ames & Schweinf. Sched. Orch. 10:81. 1930.

Epiphytic herbs. Pseudobulbs, leaves, and roots superficially identical with those of *Catasetum eburneum*. Inflorescence an arching raceme from the base of the pseudobulb, 20–30 cm. long. Flowers perfect, 8–13, pedicellate, the smallest of the genus in Panama, pure waxy white, inner lip spotted purple, strongly fragrant. Sepals subequal, free, somewhat fleshy, very strongly reflexed; dorsal sepal ligular, rounded or subacute, 1.7–2.3 cm. long and .5–1.0 cm. wide, the laterals similar, 1.8–2.3 cm. long and .4–1.0 cm. wide. Petals somewhat fleshy, very strongly reflexed, elliptic-ovate, acute, often with involute margins, 1.5 cm. long and 1–1.4 cm. wide. Lip entire, the saccate base very fleshy, ovate, acute, with thinner margins and apex, adnate to the base of the column, 1.5–1.6 cm. long and 1–1.2 cm. wide; the basal concavity surrounded by a conspicuous semicircular ridge, with an angulate, submarginate apex. Column very fleshy, 6–8 mm. long and 5–6 mm. wide. Anther with obtuse lateral lobules, the apex apiculate.

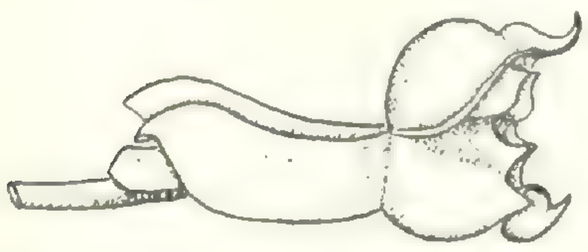


Fig. 161. *Catasetum suave*—single flower

Costa Rica and Panama.

VERAGUAS: Cerro Tuté, region west of Santa Fé, 3000 ft., *Allen 4565*.

An apparently rare species in Panama, known from a single specimen collected in the mountains of Veraguas and flowered in Gamboa.

Mansfeld, in his monograph of the genus, considers this species, as well as *C. eburneum*, as being identical with *Catasetum dilectum* Rchb. f. Careful comparison of our specimens with Reichenbach's description and figure has disclosed wide discrepancies in nearly every detail of size and structure. Neither of our Panama species have the flat, apiculate lip, subcapitate inflorescence, or pubescent rachis ascribed by Reichenbach to *Catasetum dilectum*.

5. CATASETUM VIRIDIFLAVUM Hook. in Bot. Mag. *t. 4017*. 1843.

Catasetum serratum Lindl. in Bot. Reg. n. s. 10: post *t. 24*. 1847.

Epiphytic herbs with robust fusiform pseudobulbs 8–25 cm. tall and 2–4.5 cm. wide, identical in vegetative appearance with those of *Catasetum Oerstedii*. Leaves 6–12, plicate, elliptic-lanceolate, acuminate, distichous, 20–45 cm. long and 5–12 cm. wide, the prominent veins persisting as stout spines at the apex of the imbricating bases after the leaf blades have fallen, most noticeable at the apex of the older pseudobulbs where they form a dense spinous cluster. Roots stout, with erect, slender, spinous, secondary rootlets which form a dense mat about the base of the pseudobulbs. Inflorescences erect or arching racemes produced from the base of the pseudobulbs, 25–70 cm. long. Flowers dimorphic, unisexual, the staminate and pistillate forms borne on separate scapes. Staminate flowers: those most frequently seen, 2–12, relatively large and conspicuous. Sepals membranaceous, free, subequal, pale green aging yellow, the dorsal sepal concave, elliptic-lanceolate,

Fig. 162. *Catasetum viridiflavum*

acute, 3.5–5 cm. long and 1.0–2.5 cm. wide, the laterals spreading, oblanceolate, acute, 4.5–5 cm. long and 1.5–3.0 cm. wide. Petals membranaceous, pale green aging yellow, ovate, acute, 3.5–4.5 cm. long and 2–3 cm. wide, the inner margins somewhat overlapping, forming with the dorsal sepal a concave trough under the column. Lip very firm, fleshy, globose, 3–3.5 cm. long and 3–3.5 cm. broad, with an abrupt, conical basal constriction, outer surface glabrous, yellow, the lateral margins minutely ciliate, pale green, aging yellow, apex obscurely emarginate; inner lip orange, strongly rugose-striate, terminating in a spreading fleshy callus just below the apex. Column rostrate, arcuate, broadly winged, 3.5 cm. long and 1.2 cm. broad, the under-surface with 2 elongate antennae, one usually unciform, the tip of the other extending nearly to the inner base of the lip. Anther rostrate; pollinia normal, ejected with considerable force on the slightest disturbance of the anther or antennae. Pistillate flowers relatively infrequent, 2–4 on an erect raceme. Sepals subequal, fleshy, green, spreading or reflexed, the dorsal sepal rectangular, obtuse or broadly acute, 1.5–2 cm. long and 1–1.2 cm. wide, the laterals broadly ligular, obliquely acute, 2–2.5 cm. long and 1.0–1.2 cm. broad. Petals fleshy, green, erect or reflexed, elliptic-lanceolate, acute, 2–2.5 cm. long and 1.2–1.5 cm. broad. Lip fleshy, firm, calceiform, 3–4 cm. long and 2.5–2.7 cm. broad, green on the outer surfaces, aging greenish yellow within, glabrous throughout. Column fleshy, very short, stout, 8–10 mm. long and 8–10 mm. broad, roughly triangular in cross-section, green or greenish yellow. Stigma normal.

Panama.

CANAL ZONE: Barro Colorado Island, Gatún Lake, *Woodworth s. n.*; vic. Nuevo Limón, *Babbitt s. n.*; Barro Colorado Island, *Kennoyer 252, 253;* Frijoles, *Powell 3556;* among floating islands, north arm of Gigante Bay, *Dodge 3482;* vic. Gamboa, 100 ft., *Allen 5149.* PANAMÁ: vic. Arenoso, lower Río Trinidad, 26–50 m., *Seibert 597;* Bella Vista, sea level, *Killip 12040;* drowned forest near Vigía and San Juan, Río Pequení, 66 m., *Dodge, Steyermark & Allen 16591;* hills northeast of La Joya, 50–300 m., *Dodge et al. 16904;* Pacora, 50 m., *Allen 4502, 4524, Fairchild s. n.;* San José Island, Perlas Archipelago, *Johnston 333.* COCLÉ: hills south of El Valle de Antón, 2000 ft., *Fairchild s. n.*

A very frequent species, apparently confined to the lowlands in the eastern half of the Republic.

6. CATASETUM WARCZEWITZII Lindl. & Paxt. in Paxton's Flow. Gard. 1:45, *fig. 29.* 1850–51.

Catasetum scurra Rchb. f. in Gard. Chron. 1003. 1872.

Dwarf epiphytic herbs, with clustered, stout, ovate, acute pseudobulbs 3–9 cm. tall and 2–4 cm. wide, often becoming conspicuously ridged and wrinkled with age, nearly identical in appearance with those of *Catasetum bicolor.* Leaves 4–6, elliptic-lanceolate, plicate, ultimately deciduous, 12–40 cm. long and 2.5–8 cm. wide, the broad imbricating bases enveloping the pseudobulbs, persistent for a year or more after the blades have fallen, drying grayish white, the strong midribs projecting beyond the old suture line as sharp spines, clustered at the apex of the

old pseudobulbs. Inflorescences laxly pendent, unbranched racemes from the base of the pseudobulbs. Flowers perfect, 5–8, relatively large and conspicuous. Sepals membranaceous, white or greenish white, striped pale green, dorsal sepal concave, erect, ovate, obtuse, 10–12 mm. long and 8–10 mm. broad, laterals spreading, adnate at the base, obliquely ovate, obtuse, 15–18 mm. long and 10–14 mm. wide. Petals membranaceous, subequal to the sepals, white or greenish white, striped pale green, spreading, concave, ovate, obtuse, 10–12 mm. long and 10–12 mm. wide. Lip 3-lobed, white or greenish white, striped pale green, the base saccate and somewhat fleshy, hinged to the base of the column, the lateral lobes erect, the anterior margins spreading, fimbriate, mid-lobe reflexed, the apex strongly fimbriate. Column short, the under-surface without antennae, inflated at the apex, 6–7 mm. long.

Costa Rica, Panama, Colombia, and Venezuela.

CANAL ZONE: Gatún Lake, sea level, *Powell 60;* Frijoles, sea level, *Powell 3477.* PANAMÁ: Río La Maestra, 0–25 m., *Allen 57;* drowned forest below the Río Indio Hydrographic station, 70 m., *Steyermark 17379;* without definite locality, *Pring s. n.* COCLÉ: El Valle de Antón, 600 m., *Allen 3916;* El Valle, 1800 ft., *Fairchild s. n.*

A frequent species found in the lowlands of both coasts, and at least on the Pacific slope up to about 3000 ft. elevation.

48. CYCNOCHES Lindl.

CYCNOCHES Lindl. Gen. & Spec. Orch. Pl. 154. 1832; Benth. & Hook. Gen. Pl. 3:552. 1883; Schltr. in Orchis 10:47–61. 1916.

Epiphytic herbs with short or elongate, often slightly undulate pseudobulbs of uniform thickness, tapering at the apex. Leaves few to many, distichous, lanceolate, acuminate, plicate, the blades deciduous, the unarmed, imbricating, persistent, grayish white papery bases tightly enveloping the stems. Inflorescences arching or pendent, unbranched racemes, produced in succession from the upper leaf axils while the plants are still in leaf, or from near the apex of the upper imbricating leaf bases after the blades have fallen. The species of the genus fall into two well marked subgeneric sections. In EUCYCNOCHES, which contains the generic type: both staminate and pistillate flowers large and conspicuous, usually produced on separate scapes, although mixed inflorescences containing both forms may rarely be seen. Sepals and petals in both sexes similar, fleshy or membranaceous, erect or reflexed, the lip in both fleshy, without marginal teeth. Structural differences in this section almost entirely confined to the column, that of the staminate flowers very slender, terete, elongate, and arcuate, bearing the anther at the apex, without a functional stigma or ovary; the pistillate column short, stout, fleshy, more or less winged, particularly at the apex, without an anther, but with a normal stigma and ovary. In HETERANTHAE: staminate and pistillate flowers strikingly dissimilar in size, color and structure, usually produced on separate scapes although mixed inflorescences are rarely seen. Pistillate flowers relatively large and fleshy,

similar in structure to those of the subgenus EUCYCNOCHES, usually produced on short, arching, few-flowered racemes. Staminate flowers small, on elongate, often dense, pendent racemes. Sepals and petals membranaceous, spreading or reflexed, often undulate, the lip reduced to a small ligular, triangular or rounded, usually concave disk, margined by long or short-pointed, forked, rounded or clavate teeth. Column slender, terete, arcuate. In both subgeneric sections the anther of the staminate form is terminal, operculate, incumbent, 1-celled or imperfectly 2-celled; pollinia 2, waxy.

An extremely interesting but poorly understood genus of American epiphytic orchids ranging from Mexico to Peru and Brazil. Schlechter's revision, published in 1916, lists sixteen species, to which some nine or ten have been added to date. Present evidence would indicate that of this considerable total about ten actually represent fairly consistent and valid entities, six of which are known to occur in Panama.

a. Both staminate and pistillate flowers large, nearly identical except for the column. Lip of both sexes very fleshy, with a membranaceous margin or apex, that of the staminate flowers without marginal teeth (Subgenus EUCYCNOCHES).
  b. Lip sessile or nearly sessile, broadly elliptic-lanceolate, acute, convex, nearly twice as long as broad, with a narrow, ovate, obtuse depression below the projecting triangular, basal callus ..... 2. C. CHLOROCHILON
 bb. Lip truly clawed at the base, strongly ventricose.
    c. Basal claw of the lip elongate; basal callus broadly obtuse at the apex, not projecting, the surrounding blotched area not depressed .. 6. C. VENTRICOSUM
   cc. Basal claw of the lip short; basal callus triangular, acute, projecting, the surrounding area with a broadly lunate depression ..... 5. C. TONDUZII
aa. Staminate and pistillate flowers strikingly dissimilar; pistillate flowers fleshy, relatively large, the lip nearly flat or slightly convex; staminate flowers small, membranaceous, in short or elongate, pendent racemes. Lip truly clawed at the base, the mid-portion concave, with marginal teeth (Subgenus HETERANTHAE).
  b. Staminate flowers relatively large. Sepals and petals spreading or only the apices recurved. Lip 2–2.5 cm. long, ovate, the basal concavity elliptic, broadly lanceolate. Marginal teeth slender, elongate, usually forked at the apex ..... 1. C. AUREUM
 bb. Staminate flowers relatively small. Sepals and petals usually strongly recurved and often undulate or revolute. Lip about 1–1.5 cm. long, the basal concavity ovate to orbicular, terminating in a slender lanceolate or ligular apex. Marginal teeth usually rounded or clavate, sometimes forked at the apex.
    c. Marginal teeth very short, rounded or subclavate, inconspicuous in dried specimens ..... 3. C. DIANAE
   cc. Marginal teeth elongate, truncate, clavate, or rarely forked at the apex, very conspicuous in dried specimens ..... 4. C. EGERTONIANUM

1. CYCNOCHES AUREUM Lindl. & Paxt. in Paxton's Flow. Gard. 3:6, *t. 75*. 1852–53.

Erect epiphytic herbs with stout or slender, cylindric pseudobulbs of uniform thickness, tapering at the apex, 15–30 cm. tall and 2–6 cm. wide; larger, very robust plants infrequently found growing on decaying wood and differing very considerably in superficial appearance from the more familiar slender type. Leaves

6–10, lanceolate, acuminate, plicate, ultimately deciduous, the unarmed, persistent, grayish white, papery, sheathing bases tightly enveloping the stems. Inflorescences produced from the upper half of the pseudobulb, usually either all staminate or all pistillate flowers, although mixed scapes are infrequently seen. Staminate flowers those most frequently produced: relatively large, 6–8 cm. in diameter when spread out, usually borne on long pendulous racemes. Sepals subequal, membranaceous, spreading, only the apices reflexed, pale yellowish green, sometimes veined darker green or nearly white, with minute rose-red spots, dorsal sepal erect, oblanceolate, acute, 3.5–4 cm. long and 1.0–1.2 cm. wide, laterals spreading, elliptic-lanceolate, acute, 3–3.5 cm. long and 1.5–1.8 cm. broad. Petals spreading, oblanceolate, acute, somewhat oblique, colored like the sepals, 3.5–3.8 cm. long and 1.4–1.6 cm. broad. Lip membranaceous, ovate or triangular, acute, white, often obscurely striped green, the middle concavity including the apex 2–2.5 cm. long and 1–1.2 cm. wide, the lateral margins with elongate, slender, arcuate teeth, most of which are forked at the apex, the base of the middle concavity with 2 erect fleshy elongate truncate crests. Column slender, arcuate, terete, 3.5 cm. long, dilated at the apex; pollinia 2, waxy. Pistillate flowers: relatively infrequent, usually 2–4 on short arching scapes, or rarely subtended by several to many of the staminate form, fleshy throughout. Sepals free, spreading, subequal, yellowish green, obscurely veined darker green, the dorsal sepal 4.5–5.5 cm. long and 1.8–2.2 cm. wide, the laterals 4.5–5 cm. long and 1.8–2 cm. wide. Petals similar to the sepals but broader, 3.5–4 cm. long and 2.2–2.5 cm. broad. Lip very fleshy, slightly convex, ovate, acute, greenish yellow shading to green at the apex, about 3 cm. long and 2.0–2.2 cm. wide, with a basal brown lunate crest. Flowers aging greenish yellow, with narrow brown margins to all segments. Column very stout, about 15 mm. long and 4 mm. in diameter at the terete base, the truncate apex dilated, very variable in width, with a triangular or auriculate fleshy wing on each side of the stigmatic surface.

Costa Rica and Panama.

COCLÉ: El Valle de Antón, 800 m., *Koerber s. n.*; region north of El Valle de Antôn, 2000 ft., *Allen 5166;* floor of El Valle de Antón, 600 m., *Allen 3628;* El Valle Chiquito, headwaters of the Río Mata Ahogado, 900 m., *Dunn s. n.* (under *Allen 3800*).

2. CYCNOCHES CHLOROCHILON Klotzsch, in Allgem. Gartenzeit. 6:225. 1838.

Cycnoches Warszewiczii Rchb. f. in Bot. Zeit. 10:734. 1852.

Erect epiphytic herbs, with pseudobulbs and leaves typical of the genus. Inflorescences usually of all staminate or all pistillate flowers. Flowers in either case large and fleshy, differing from one another only in the structure of the column; lip sessile or very nearly so. Staminate flowers those most frequently seen: Sepals subequal, free, spreading, yellowish green, the dorsal sepal erect, lanceolate, acute, concave, 9–11 cm. long and 1.6–1.7 cm. wide, laterals spreading, subfalcate, lanceolate, acute, 6.5–7.5 cm. long and 1.4–1.6 cm. wide. Petals spreading, ellip-

Fig. 163. *Cycnoches aureum*

tic-lanceolate, subfalcate, acute, yellowish green, 7–8 cm. long and 2–2.5 cm. wide. Lip fleshy, sessile or very nearly sessile at the base, elliptic-lanceolate, acute, convex toward the middle, not strongly ventricose, 6–6.5 cm. long and 2.5–3.2 cm. wide, white with a dark green, ovate, obtuse depression below the fleshy, triangular, acute, projecting, dark green, basal callus. Column elongate, slender, terete, arcuate, 2.8–3.2 cm. long, dilated at the apex. Anther and pollinia normal. Pistillate flowers less frequently seen: identical with the staminate except for the structure of the column, which is short and stout with two fleshy, auriculate, lateral wings at the apex; stigma normal.

Panama, Colombia, Venezuela, and the Guianas.

PANAMÁ: Río La Maestra, 0–25 m., *Allen 65*. CHIRIQUÍ: Cordillera, *von Warscewicz*.

A South American species, having its northern limit of known distribution in Panama, where it apparently is rare. It is distinguished from the common *Cycnoches Tonduzii* of Chiriquí and Veraguas Provinces by the somewhat larger flowers, the sessile or very nearly sessile, elliptic-lanceolate, convex, not strongly ventricose lip, and the ovate, obtuse depression below the basal callus. Although *Cycnoches chlorochilon* has been collected in Panama only twice, it is to be expected particularly east of the Canal Zone and in Darien Province.

3. CYCNOCHES DIANAE Rchb. f. in Bot. Zeit. 10:636. 1852.

Cycnoches Powellii Schltr. in Fedde Rep. Sp. Nov. Beih. 17:58. 1922.

Erect epiphytic herbs with slender cylindric pseudobulbs 15–30 cm. tall and 2–3 cm. in thickness. Leaves plicate, deciduous, typical of the genus. Staminate inflorescences those most frequently seen, usually densely flowered, elongate and pendulous: Sepals membranaceous, free, subequal, rosy pink with white shadings, dorsal sepal erect, undulate, the apex recurved, lanceolate, acute, 2.3–2.6 cm. long and .7–.9 cm. wide, laterals often strongly reflexed, the apices recurved, lanceolate, acute, 2–2.2 cm. long and .6–.8 cm. wide. Petals membranaceous, colored similarly to the sepals, spreading, the apical halves very strongly recurved or revolute, elliptic-lanceolate, acute, 2–2.2 cm. long and 0.9–1.1 cm. wide. Lip membranaceous, truly clawed at the base, middle concavity white, orbicular, lateral margins crenate or with very short rounded or subclavate teeth, apex linear-lanceolate, acute, about equaling the middle concavity in length, base of the middle concavity with 2 erect, fleshy, ligular crests. Column very slender, arcuate, dilated at the apex. Anther and pollinia normal. Pistillate flowers relatively large and fleshy, nearly identical with those of *Cycnoches aureum*, produced on short, arching, few-flowered racemes, or rarely subtended by few or many of the smaller staminate form.

Panama, and probably Costa Rica.

CHIRIQUÍ: Caldera River, 4500 ft., *Powell 186*; Chorch Berg, 3000–4000 ft., *Warscewicz s. n.*

This species seemingly is recorded only from the intermediate highlands of Chiriquí Province in Panama, although it is to be expected in adjacent Costa Rica. It differs from the closely related *Cycnoches Egertonianum* in the much shorter marginal teeth on the lip of the male flowers.

4. CYCNOCHES EGERTONIANUM Batem. Orch. Mex. et Guat. *t. 40* (in part). 1837–42.

Cycnoches ventricosum var. *Egertonianum* Hook. in Bot. Mag. *t. 4054.* 1844.
Cycnoches stelliferum Lodd. in Cat. Orch. 25. 1844 (nom. nud.); Lindl in Bot. Reg. n. s. 9: sub *t. 46,* in syn. 1846.
Cycnoches glanduliferum Rich. & Gal. ex Hemsl. in Gard. Chron II, 11:268. 1879.
Cycnoches peruvianum Rolfe, in Lindenia 7:29, *t. 301.* 1891.
Cycnoches Rossianum Rolfe, in Gard. Chron. III, 9:456. 1891.
Cycnoches densiflorum Rolfe, in Kew Bull. 63. 1909.
Cycnoches guttulatum Schltr. in Fedde Rep. Sp. Nov. Beih. 17:56. 1922.
Cycnoches pachydactylon Schltr. loc. cit. 57. 1922.
Cycnoches stenodactylon Schltr. loc. cit. 59. 1922.
Cycnoches Amparoanum Schltr. loc. cit. 19:48. 1923.
Cycnoches pauciflorum Schltr. loc. cit. 137. 1923.

Epiphytic herbs, typical of the genus, nearly identical with *C. aureum* and *C. Dianae.* Flowers dimorphic, unisexual. Staminate flowers those most frequently seen, produced in long, dense, pendent racemes from the upper half of the pseudobulbs: sepals membranaceous, subequal, green suffused purple on the frontal surfaces, or more frequently green or greenish tan spotted with red-brown, maroon or purple, dorsal sepal erect, lanceolate, acute, the apex often recurved, 2.5–3 cm. long and .5–.7 cm. wide, the laterals spreading, elliptic-lanceolate, acute, often with the apical half strongly revolute, 2–2.5 cm. long and .6–1.0 cm. wide. Petals membranaceous, colored similarly to the sepals, spreading, the apical half usually strongly revolute, elliptic-lanceolate, acute, 2–2.5 cm. long and 1–1.2 cm. wide. Lip membranaceous, truly clawed at the base, green tinged purple to pure white, the middle concavity ovate to orbicular, the lateral margins with elongate, rounded, clavate, or rarely forked teeth, equaling or exceeding the middle concavity in length; apical lobe lanceolate, acute or acuminate, the base of the middle concavity with 2 erect, truncate or subclavate, fleshy crests. Column slender, terete, arcuate, 2 cm. long, dilated at the apex. Anther normal; pollinia 2, waxy. Pistillate flowers relatively large, fleshy, borne on short, arching, few-flowered racemes, nearly identical with those of *Cycnoches aureum.*

Mexico, Guatemala, Honduras, Costa Rica, Panama, Colombia, Peru, and Brazil.

CANAL ZONE: Balboa, *Powell 159;* lake shore along Gatún River valley, *Pittier 6802;* Gatún Lake and other low places, under 100 ft., *Powell s. n.* PANAMÁ: hills near city, sea level, *Powell s. n.* COCLÉ: El Valle de Antón, 1000 m., *Allen 3639;* floor of El Valle, 600 m., *Allen 3627,* 650 m., *Dunn s. n.;* El Valle Chiquito, 1800–2000 ft., *Allen 4500, 5080, 5162.* CHIRIQUÍ: without definite locality, 3000–3500 ft., *Powell 173.*

A frequent species, somewhat variable in the color of the male flowers and in the relative number, length, and termination of the apex of the marginal teeth of

the lip. Much has been made of these differences, but a considerable amount of field observation in Panama, Costa Rica, and Honduras, together with careful examination of the now fairly adequate collections, discloses that scarcely any two specimens are exactly alike in these characters, even within the limits of the so-called species. It is rather significant that most of these species have been described from single specimens, or from several inflorescences produced in cultivation probably from the same plant.

5. Cycnoches Tonduzii Schltr. in Fedde, Rep. Sp. Nov. Beih. 19:298. 1923.

Epiphytic herbs, the more robust plants usually found growing on decaying wood or where they have been fertilized in some manner. Pseudobulbs slender, often somewhat undulate, uniformly cylindric, tapering at the apex, 15–70 cm. tall and 2.5–4 cm. wide. Leaves distichous, broadly lanceolate, plicate, the blades ultimately deciduous, 15–45 cm. long and 2–10 cm. wide, the unarmed, persistent, grayish or greenish white, papery, closely imbricating bases tightly enveloping the stems. Inflorescences few to many, usually produced in succession from the upper leaf axils either while the leaves are present or after they have fallen. Flowers quite variable in size. Staminate and pistillate flowers identical in structure except for the column, usually produced on separate arching or pendent racemes. Staminate flowers those most frequently seen: sepals free, spreading, fleshy, green aging greenish yellow, the dorsal sepal erect, lanceolate to elliptic-lanceolate, acute, concave, 4–7 cm. long and 1–2 cm. broad, the tip often recurved, laterals spreading, subfalcate, acute, 4–6 cm. long and 1.5–2.5 cm. wide. Petals fleshy, spreading, elliptic-lanceolate, subfalcate, acute, green aging greenish yellow, 4–6 cm. long and 1.8–3.5 cm. broad. Lip shortly clawed at the base, ovate, obovate, or subcordate, 3.5–4 cm. long and 1.8–3.5 cm. wide, pure white, mid-portion very fleshy, strongly ventricose, the apex and lateral margins somewhat recurved, membranaceous; basal callus fleshy, dark green, triangular, acute, conspicuously projecting, surrounded by a dark green lunate depression. Column very slender, arcuate, 2.2–3.5 cm. long, terete, the apex dilated and rather triangular in cross-section; anther normal; pollinia 2, waxy. Pistillate flowers relatively infrequent, usually 2–4 on short arching racemes, identical with the staminate form except for the column: column stoutly arcuate, 2–2.5 cm. long and 5–6 mm. in thickness at the terete mid-portion, dilated and truncate at the apex, with a triangular or auriculate fleshy wing on each side of the normal stigma.

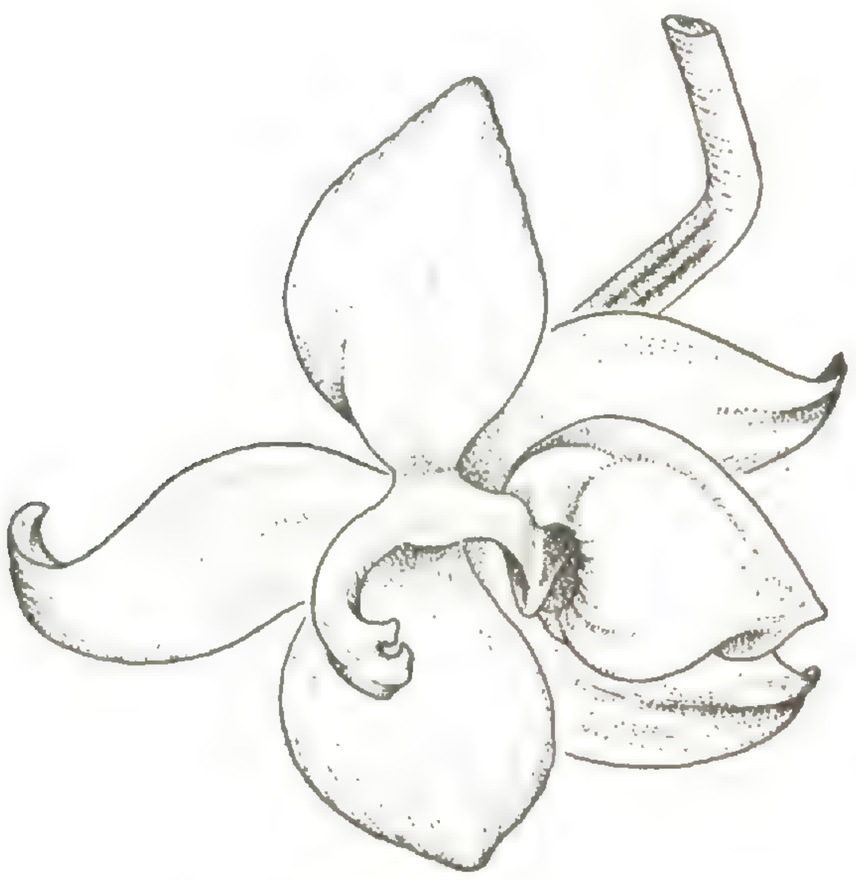


Fig. 164. *Cycnoches Tonduzii*—pistillate flower

Costa Rica and Panama.

COCLÉ: El Valle de Antón, lower portion of the valley and marshes along the Río Antón, 500 m., *Hunter & Allen 433*. VERAGUAS: vic. Río Tabasará, on large trees in open pastures, 100 m., *Allen 3913, 3914, 3915, 3979*. CHIRIQUÍ: Río Tabasará, 50 m., *Allen 2930;* Concepción, 1000 ft., *Allen 5154;* vic. Gualaca, 500 ft., *Allen 5153;* vic. Progreso, 1000 ft., *Dunn s. n.;* vic. Dolega, 1000 ft., *Dunn s. n.;* same locality, *Powell 3497*.

Fig. 165. *Cycnoches Tonduzii*

The species is quite variable in regard to size of plant, size of flower, and in the relative length and width of the lip. The larger-flowered forms are among the most attractive of all orchids, combining delicacy of color with exquisite form and fragrance.

The identity of this frequent and attractive species of western Panama and Costa Rica is a controversial issue. The flowers differ from *Cycnoches ventricosum* in the much shorter basal claw and in the conspicuous triangular basal callus, and from *C. chlorochilon* in the uniformly smaller flowers, longer basal claw, lunate, not ovate obtuse depression below the basal crest, and the strongly ventricose lip. The name *C. Warszewiczii* of Reichenbach has been used, but all present evidence indicates that this name is referable to *C. chlorochilon*.

6. Cycnoches ventricosum Batem. Orch. Mex. et Guat. *t. 5, 40* (in part). 1837–42.

Erect epiphytic herbs. Plants typical of the genus. Staminate and pistillate flowers identical except for the column. Staminate flowers those most frequently seen: sepals and petals membranaceous, green aging greenish yellow, strongly reflexed. Lip white, with an elongate basal claw, ovate, acute, the fleshy mid-section strongly ventricose, usually without thinner lateral margins, the apex membranaceous. Basal callus broadly rounded, not projecting, the surrounding lunate, dark green blotch not depressed.

Mexico, Guatemala, Honduras, and Panama.

Panamá: definite locality unknown, *Fairchild s. n.*

The citation of this species, which hitherto has been known only from Mexico and northern Central America, is based on flowers preserved in liquid from two plants flowering in the collection of Dr. Graham Fairchild. Dr. Fairchild was of the opinion that the plants had been collected originally in the lowlands of Veraguas Province.

49. COELIOPSIS Rchb. f.

Coeliopsis Rchb. f. in Gard. Chron. 9. 1872.

Epiphytic herbs superficially resembling plants of *Acineta*. Pseudobulbs stout, ovoid or subcylindric, with 3–4 plicate, prominently veined, oblanceolate, acuminate leaves at the apex. Inflorescences short, pendent, dense, subcapitate racemes from the base of the pseudobulbs. Flowers few to about 15, waxy white. Sepals very fleshy, the dorsal sepal free, concave, arching over the column, laterals connate at the base, forming a conspicuous mentum. Petals much narrower than the sepals. Lip 3-lobed, the lateral lobes erect with spreading apices, mid-lobe rectangular or ovate, longer than broad, truncate or obtuse, strongly reflexed, with ciliate margins. Column short, subclavate, obtuse, winged. Anther terminal, operculate, imperfectly 2-celled; pollinia 2, waxy.

A monotypic genus of epiphytic orchids known only from Panama and Costa Rica.

1. COELIOPSIS HYACINTHOSMA Rchb. f. in Gard. Chron. 9. 1872.

Epiphytic herbs. Pseudobulbs stout, ovoid or subcylindric, often longitudinally wrinkled, 6.5–8.5 cm. long and 2.5–4 cm. wide, the base usually enveloped in 3–5 brown, papery, closely imbricating bracts, the apex truncate, unarmed, with 3–4 oblanceolate, acuminate, plicate, prominently veined leaves 30–50 cm. long and 2–7 cm. wide. Inflorescences 4–5 cm. long, pendent, subcapitate racemes produced from the base of the pseudobulbs, basal portion tightly enveloped in the papery brown, imbricating bracts. Flowers few to about 15. Sepals white, very fleshy, the dorsal sepal free, concave, ovate, acute, 18–20 mm. long and 9–12 mm. wide, arching over the column; laterals connate at the base, forming a conspicuous mentum, the apices spreading, obliquely lanceolate, acute, 20–22 mm. long and 10–12 mm. wide. Petals white, lanceolate, acute, 15–16 mm. long and 5–6 mm. wide. Lip 3-lobed, 1.6–1.8 cm. long and 1.2–1.4 cm. wide, white, the inner lip with an orange spot, lateral lobes erect, with spreading, ciliate, apical margins, mid-lobe rectangular or ovate, truncate or obtuse, strongly reflexed, with ciliate margins. Column short, 9–11 mm. long, subclavate, winged, obtuse, white with a small purple blotch at the base. Anther pure white.

Panama and Costa Rica.

PANAMÁ: Cerro Campana, cloud forest, 3000 ft., *Allen 5184*. COCLÉ: hills north of El Valle de Antón, about 1000 m., *Allen 2402*. CHIRIQUÍ: without definite locality, *Powell 423*.

A fairly frequent species in wet, intermediate, highland forests of Panama and Costa Rica.

49-A. ERIOPSIS Lindl.

ERIOPSIS Lindl. in Bot. Reg. n. s. 10: post *t. 9*, *t. 18*. 1847; Benth. & Hook. Gen. Pl. 3:545. 1883.

Pseuderiopsis Rchb. f. in Linnaea 22:852. 1849.

Epiphytic herbs with pyriform or elongate pseudobulbs, the apex usually with 2 broad, plicate, strongly veined leaves. Inflorescences erect or arching, unbranched racemes from the base of the pseudobulbs. Flowers few to many. Sepals subequal, spreading, free, or the laterals connate at the base, forming a short mentum with the foot of the column. Petals subequal to the sepals. Lip 3-lobed, the laterals erect, the mid-lobe small, spreading, entire or 2-lobed; base of lip attached to the foot of the column; disk lamellate. Column elongate, semiterete, somewhat arcuate, dilated or subclavate but not winged; base produced into a short foot. Anther terminal, operculate, incumbent, 1-celled; pollinia 2 or 4, waxy.

A small genus of epiphytic highland orchids ranging from Costa Rica to Peru and Brazil. A single species is known to occur in Panama, the few plants found to date all unfortunately being sterile. This species is, however, sufficiently distinctive even when not in flower to be cited without hesitation.

1. ERIOPSIS RUTIDOBULBON Hook. in Bot. Mag. *t. 4437*. 1849.

Epiphytic herbs with stout, pyriform pseudobulbs which are nearly black and covered with innumerable fine wrinkles, the apex with 2–3 broadly lanceolate, acute or shortly acuminate, subcoriaceous, plicate, strongly veined leaves. Inflorescences erect or arching, unbranched racemes 30–45 cm. long, produced from the base of the pseudobulbs. Flowers few to many. Sepals subequal, free, spreading, dull orange-yellow with red-purple margins, the dorsal sepal linear-lanceolate, obtuse or shortly acute, 1.6–1.8 cm. long and .5–.6 cm. wide, laterals elliptic-lanceolate, acute, 1.6–1.8 cm. long and .5–.6 cm. wide. Petals subequal to the sepals, similarly colored, lanceolate, acute, 1.5–1.7 cm. long and .35–.4 cm. wide. Lip 3-lobed, 1.5–1.8 cm. long and .9–1.1 cm. wide when spread out, the lateral lobes rounded, dull orange-red spotted dark purple, the mid-lobe spreading, emarginate or 2-lobed at the apex, white spotted dark purple; disk with erect fleshy keels. Column 9–11 mm. long, subclavate, somewhat arcuate, greenish.

Panama, Colombia, and Peru.

Sterile plants of what in all probability are this species have been seen in recent years in Chiriquí Province at about 6000 ft. elevation, and more frequently in the wet forested region north of El Valle de Antón, in Coclé. It seems to be a rare plant.

50. SIEVEKINGIA Rchb. f.

SIEVEKINGIA Rchb. f. Beitr. Syst. Pfl. 3. 1871.

Epiphytic herbs, with pseudobulbs ovoid or subcylindric, monophyllous or rarely diphyllous at the apex. Leaves plicate, lanceolate or elliptic-lanceolate, acute, or shortly acuminate. Inflorescences short or elongate, pendent or rarely arching racemes from the base of the pseudobulbs. Flowers few to many. Sepals free, concave, spreading, subequal. Petals subequal to the sepals but usually narrower. Lip rhombic to ovate, or obovate-triangular, the lateral margins erect, the apex usually acute and spreading; disk with erect lamellae, or basal, elongate, denticulate processes. Column subarcuate, broadly winged or dilated. Anther terminal, operculate; pollinia 2, waxy.

A small genus of American epiphytic orchids ranging from Costa Rica to British Guiana and Colombia to Ecuador and Peru. They are seldom collected, perhaps because they are often mistaken for immature *Stanhopea* seedlings. A single species has been found in Panama.

1. SIEVEKINGIA SUAVIS Rchb. f., Beitr. Syst. Pfl. 3. 1871.

Dwarf epiphytic herbs. Pseudobulbs ovate, somewhat angulate, 1.5–3 cm. tall and 1.0–1.5 cm. wide, sheathed at the base in 2–3 papery bracts, the apex with

a single lanceolate or elliptic-lanceolate, acute or shortly acuminate, plicate, subcoriaceous leaf 8–25 cm. long and 1.5–3.2 cm. wide. Inflorescences short, pendent racemes produced from the base of the pseudobulbs. Flowers about 6 or fewer. Sepals subequal, free, spreading, pale lemon-yellow, dorsal sepal concave, elliptic-lanceolate, acute, 10–17 mm. long and 4–8 mm. wide; laterals concave, elliptic-lanceolate, acute, 12–17 mm. long and 4–8 mm. wide. Petals orange, lanceolate, acute, 10–15 mm. long and 3–6 mm. wide. Lip ovate or obovate-rhombic when spread out, 8–11 mm. long and 6–10 mm. wide, orange with reddish purple spots, subnavicular, the lateral margins erect, the apex acute and spreading; disk with 3 prominent or obscure, erect keels, the central keel prolonged and terminating in an inconspicuous 2-lobed scale. Column somewhat arcuate, 6–8 mm. long, green, broadly winged, the wings orange.

Costa Rica and Panama.

COLÓN: Cativo-Porto Bello trail, sea level, *Powell 379;* Río Llano Sucio, vic. Puerto Pilón, 100 m., *Butcher s. n.* (under *Allen 2841*).

Apparently a rare species. The Panama specimens are consistently smaller in all respects than those seen from Costa Rica, but other than in size there seem to be no differences.

51. KEGELIELLA Mans.

KEGELIELLA Mans. in Fedde Rep. Sp. Nov. 36:60. 1934.

Kegelia Rchb. f. in Bot. Zeit. 10:670. 1852.

Small epiphytic herbs, the plants considerably resembling those of a small *Gongora* or *Stanhopea*. Pseudobulbs ovoid, somewhat compressed, angulate, the apex with 2–3 broadly elliptic-lanceolate, acute, plicate leaves. Inflorescences pendent racemes from the base of the pseudobulbs, the rachis densely covered with glandular hairs. Flowers relatively small, about 6 or fewer. Sepals subequal, free, spreading, lanceolate or elliptic-lanceolate, acute or acuminate, covered with glandular hairs on the outer surfaces. Petals subequal to the sepals but narrower and shorter, lanceolate or oblanceolate, acute or acuminate. Lip membranaceous or fleshy, 3-lobed, the lateral lobes large, spreading or erect, obliquely angulate and subdolabriform when spread out, or broadly ovate and subtruncate toward the basal claw, mid-lobe small, subcordate or triangular, concave or flat, separated from the laterals by emarginate sinuses or plicate folds; disk with an erect, fleshy, laterally compressed or carinate, dorsally 1- or 2-sulcate, 2-lobed or acute linguiform callus. Column elongate, more or less arcuate, slender below, broadly winged above, without a foot. Anther terminal, operculate, incumbent, 1-celled. Rostellum elongate, the apex obcordate or acuminate; pollinia 2, waxy.

An extremely rare genus of American epiphytic orchids previously known from a few specimens collected in Costa Rica, Jamaica, Trinidad, and Surinam. Two species have been described, both of which have been found in Panama.

a. Lip membranaceous; apical lobe flat, spreading, conspicuously separated from the lateral lobes by marginal sinuses..... 1. K. Houtteana
aa. Lip fleshy; apical lobe concave, confluent with the laterals, separated only by plicate folds..... 2. K. Kupperi

1. Kegeliella Houtteana (Rchb. f.) L. Wms. in Ann. Mo. Bot. Gard. 29:347. 1942.

Kegelia Houtteana Rchb. f. in Bot. Zeit. 10:670. 1852.

Dwarf epiphytic herbs, with ovoid, laterally compressed, somewhat angulate pseudobulbs 1.5–2 cm. long and 1–1.5 cm. wide, the apex with 3 broadly elliptic-lanceolate, acute, plicate leaves 9–13 cm. long and 3.5–5 cm. wide. Inflorescences pendulous racemes about 10 cm. long from the base of the pseudobulbs, the rachis densely covered with minute reddish glandular hairs. Flowers few, relatively small. Sepals membranaceous, subequal, free, concave, spreading, pale yellow, the outer surfaces with minute reddish glandular hairs, dorsal sepal lanceolate, acuminate, 12–15 mm. long and 3–4 mm. wide, laterals elliptic-lanceolate, acuminate, 14–16 mm. long and 4–5 mm. wide. Petals lanceolate, acuminate, pale yellow barred red, 11–12 mm. long and 1.5–2.5 mm. wide. Lip 3-lobed, membranaceous, yellow, 9–11 mm. long and 5–7 mm. wide when spread out, lateral lobes erect, obliquely angulate or subdolabriform when spread out, mid-lobe triangular or subcordate, flat, spreading, separated from the laterals by emarginate sinuses; disk with an erect, fleshy, laterally compressed, more or less 2-lobed linguiform callus. Column 10–12 mm. long, somewhat arcuate, apple-green, slender below, broadly winged above. Anther yellow.

Panama, Jamaica, Trinidad, and Surinam.

COCLÉ: region north of El Valle de Antón, vic. of La Mesa, 1000 m., *Allen 2759*.

Sterile plants of what may also be this species have been recently collected on the upper wet forested slopes of mountains west of Santa Fé, in Veraguas. Apparently rare.

2. Kegeliella Kupperi Mansf. in Fedde Rep. Sp. Nov. 36:60. 1934.

Small epiphytic herbs with ovoid, somewhat compressed and angulate pseudobulbs 2–3 cm. long and 1–2 cm. wide, the apex with 2 elliptic-lanceolate, acute, plicate leaves 4–8 cm. long and 1.5–3 cm. wide. Inflorescences pendent racemes 9–12 cm. long, produced from the base of the pseudobulbs, the rachis densely covered with minute brown glandular hairs, at least above. Flowers relatively small, from solitary to about 6. Sepals membranaceous, subequal, free, spreading, concave, the outer surfaces densely covered with minute glandular hairs, dorsal sepal lanceolate, acuminate, 16–18 mm. long and 5–6 mm. wide, laterals elliptic-lanceolate, acuminate, 1.7–1.9 cm. long and .6–.65 cm. wide. Petals oblanceolate, acute or acuminate, 1–1.3 cm. long and 3–3.2 mm. wide. Lip 3-lobed, fleshy, the lateral lobes large, rounded, spreading, mid-lobe small, subcordate, concave, separated from the lateral lobes by plicate folds; disk with an erect, fleshy, carinate,

acute, linguiform callus. Column 10–12 mm. long, somewhat arcuate, slender below, broadly winged above.

Costa Rica and Panama.

COLÓN: Quebrada López, slopes of Cerro Santa Rita, 100 ft., *Butcher s. n.* (under *Allen 2108*).

This is apparently the second collection of this exceedingly rare species.

52. ACINETA Lindl.

ACINETA Lindl. in Bot. Reg. Misc. n. s. 6:67. 1843; Benth & Hook. Gen. Pl. 3:551. 1883; Schltr. in Orchis 11:21–48. 1917.

Neippergia C. Morr. in Ann. Soc. Roy. Agr. & Bot. Gand 5:375, *t. 282.* 1849.
Lueddemannia Rchb. f. in Bonplandia 2:281. 1854.
Luddemania Rchb. f. in Linden, Pescatorea 1, *t. 22.* 1860.
Luedemannia Benth. in Benth. & Hook. Gen. Pl. 3:552. 1883.

Stout epiphytic herbs with ovoid or subcylindric, often laterally compressed or furrowed pseudobulbs, the apex with 1–4 broadly plicate leaves, the plants considerably resembling a robust *Stanhopea*. Inflorescences elongate, pendulous or erect racemes from the base of the pseudobulbs. Flowers usually many, fleshy, relatively large and conspicuous. Sepals subequal, broadly concave, the dorsal sepal free, the laterals usually connate at the base. Petals subequal to the sepals but usually smaller. Lip 3-lobed, fleshy, concave, with a concave or subsaccate, basal claw or hypochile, lateral lobes large, erect, triangular or subreniform, the apical lobe carinate, concave or spreading; disk fleshy, with variously shaped appendages. Column erect, usually pubescent, somewhat arcuate, subclavate or narrowly winged, without a foot. Anther terminal, operculate, incumbent, 1-celled or imperfectly 2-celled; pollinia 2, waxy.

A genus of robust American epiphytic orchids ranging from southern Mexico to Venezuela and Ecuador. Vegetatively they often considerably resemble a stout *Stanhopea,* but are most closely allied to *Peristeria,* although the complex structure of the lip in some species more nearly approaches that found in the former genus.

Schlechter in his monograph distinguishes 13 species, the major separations in his key being based on color. No attempt has been made to evaluate these specific concepts, except that *Acineta chrysantha* and *A. sella-turcica* seem to be one entity on the basis of the evidence now available. Of the two valid species that have been listed for Panama, only one, *A. chrysantha,* has been found in recent years. However, the wide distribution of *A. superba* in adjacent Colombia would increase the possibility that it has been, or will be found in Panama.

a. Lip in profile with a broadly emarginate indentation or constriction below the lateral lobes, separating the hypochile from the epichile, the basal claw or hypochile subsaccate; apical lobe of the lip about 1 cm. long ..... 1. A. CHRYSANTHA

aa. Lip in profile deeply gibbous and continuous, without an emarginate indentation below the lateral lobes; basal claw or hypochile rectangular-concave, not subsaccate; apical lobe of the lip about 2 cm. long ..... 2. A. SUPERBA

1. ACINETA CHRYSANTHA (Morr.) Lindl. & Paxt. in Paxton's Flow. Gard. 1:31. 1850–51.

Neippergia chrysantha C. Morr. in Ann. Soc. Roy. Agr. & Bot. Gand 5:375, *t. 282.* 1849.
Acineta densa Lindl. & Paxt. in Paxton's Flow. Gard. 1:91. 1850–51.
Acineta sella-turcica Rchb. f. in Bot. Zeit. 10:705. 1852.
Acineta Warscewiczii Kl. in Allgem. Gartenzeit. 20:145. 1852.

Robust epiphytic herbs with ovoid or subconic, somewhat laterally compressed, more or less furrowed pseudobulbs 8–10 cm. long and 6–8 cm. wide, the apex with 3–4 broad, oblanceolate, plicate, acute leaves 30–45 cm. long. Inflorescences elongate, pendulous racemes from the base of the pseudobulbs. Flowers many, fleshy, not fully expanding, subglobose, relatively large and conspicuous. Sepals fleshy, free, not spreading, yellow, concave, dorsal sepal oblong-ovate, obtuse, 2.5–3.5 cm. long and 2–2.7 cm. wide, laterals elliptic-ovate, shortly and broadly acute, 2.5–3.5 cm. long and 2–2.8 cm. wide. Petals membranaceous, obovate, acute, yellow, spotted red particularly toward the base or on the margins, 3–3.2 cm. long and 1.8–2 cm. wide. Lip very fleshy, 3-lobed, 2.5–3 cm. long and 2.5–3 cm. broad when spread out, yellow spotted red-brown, the basal claw or hypochile broadly concave or subsaccate, terminating in a short, erect, fleshy horn; lateral lobes erect, subreniform; apical lobe short, concave or spreading, subquadrate or rhombic-obovate, acute, 8–12 mm. long and 8–12 mm. wide; disk with a broad, erect, prominent callus with 2 small, lateral, subfalcate wings, the projecting carinate, apical margin with short fleshy teeth. Column stout, pubescent, 2–2.2 cm. long, the base semiterete, the apex with narrow lateral wings.

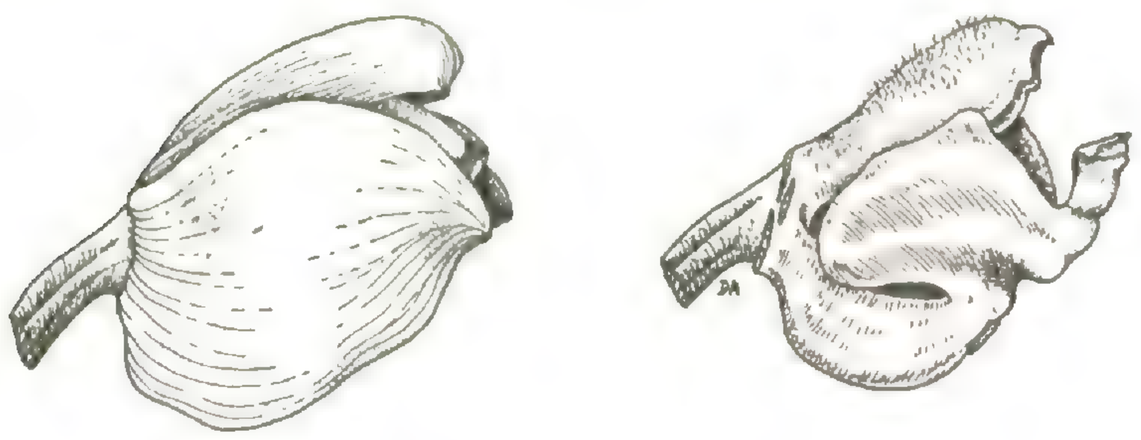


Fig. 166. *Acineta chrysantha*

Costa Rica and Panama.

CHIRIQUÍ: Indian Hill, 5000 ft., *Powell 314, 417;* without definite locality, *Pring s. n.*

Our specimens seem to differ in minor detail, particularly in the basal fleshy callus of the disk and in the upper margin of the clinandrium, from typical material of this species; but in spite of these discrepancies, they seem to compare more nearly to *A. chrysantha* than to any other.

2. ACINETA SUPERBA (HBK.) Rchb. f. in Walp. Ann. 6:609. 1863.

Anguloa superba HBK. Nov. Gen. & Sp. 1:343, *t. 93.* 1815.
Peristeria Humboldti Lindl. in Bot. Reg. n. s. 6: *t. 18.* 1843.
Acineta Humboldtii Lindl. loc. cit. Misc. 68. 1843.
Acineta fulva Kl. in Allgem. Gartenzeit. 20:146. 1852.
Acineta Colmani Hort. ex Gard. Chron. III, 35:173. 1904.

Stout epiphytic herbs with ovoid, somewhat angular pseudobulbs 7–10 cm. long and 4–6 cm. wide, the apex with 2–3 lanceolate, acute, plicate leaves 25–45 cm. long. Inflorescences elongate, pendent racemes from the base of the pseudobulbs. Flowers about 5 to numerous, fleshy, relatively large and conspicuous, not fully expanding, variable in color from pale yellow to reddish brown, with red or brownish purple spots. Sepals fleshy, concave, the dorsal sepal free, more or less erect, oblanceolate, shortly acute, 3.5–4 cm. long and 2–2.2 cm. wide, laterals connate at the base, obliquely elliptic-lanceolate, acute, 3.5–4 cm. long and 2–2.5 cm. wide. Petals membranaceous, oblanceolate-obtuse or very shortly and broadly acute, 3–3.5 cm. long and 1.8–2 cm. wide. Lip very fleshy, gibbous, 3-lobed, the basal claw or hypochile rectangular-linear, concave, the lateral lobes erect, broadly

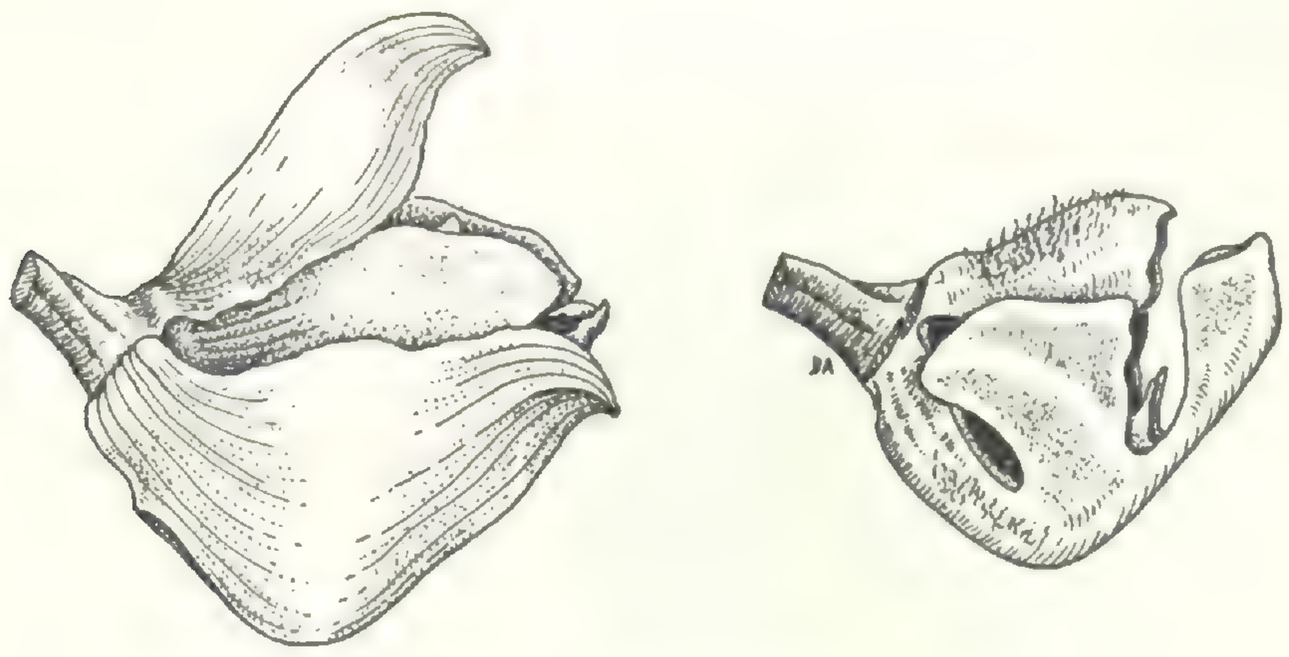


Fig. 167. *Acineta superba*

triangular, the apical lobe of the lip elongate, carinate, 1.8–2 cm. long and about 1.8–2 cm. wide when spread out, obovate, obtuse; disk with a very conspicuous, erect, oblong-quadrate, fleshy callus with 2 identical, divergent, forked processes arising from a common restricted base, the one pointing toward the apex and the other toward the base of the lip. Column stout, pubescent, 1.8–2 cm. long and 1.3–1.5 cm. wide, subterete below, narrowly winged above, the wings confluent at the apex, forming a hood over the clinandrium.

Panama?, Colombia, Venezuela, and Ecuador.

This species was first discovered by Humboldt and Bonpland in a valley called Catacocha, near Zaruma, in what is now Ecuador. It is doubtfully listed by Schlechter for Panama, although he evidently had not seen authentic specimens, nor have any been available for the preparation of this manuscript. However, its wide distribution in adjacent Colombia and northern South America would strengthen the probability that it has been found, or will be found within the limits of our area.

53. PERISTERIA Hook.

Peristeria Hook. in Bot. Mag. *t. 3116.* 1831; Benth. & Hook. Gen. Pl. 3:550. 1883.

Peristera Endl. Gen. Pl. 199. 1837.
Eckardia Rchb. ex Endl. Gen. Pl. Suppl. 2:17. 1842.

Epiphytic or terrestrial herbs, with stout ovoid or subconic pseudobulbs, the apex with 1–5 broad, elliptic-lanceolate, plicate leaves which are often deciduous. Inflorescences tall erect or short pendent racemes from the base of the pseudobulbs. Flowers fleshy, subglobose, relatively large and conspicuous. Sepals fleshy, subequal, broadly concave, the dorsal sepal usually free, the laterals somewhat connate at the base. Petals subequal to the sepals, but smaller. Lip very fleshy, with a broadly concave basal claw or hypochile which is adnate to or continuous with the base of the column, with or without a fleshy central callus, with or without elongate, erect, lateral wings; apical portion or epichile entire, articulated with the hypochile, inflexed or incumbent, lateral margins erect, spreading or retuse; disk with or without a fleshy ventricose or 2-keeled callus. Column erect, short, stout, subterete, without a foot, with or without elongate lateral projections. Anther terminal, operculate, incumbent, imperfectly 2-celled; pollinia 2, waxy.

About six species of robust epiphytic or terrestrial herbs ranging from Costa Rica and Panama to Surinam and Peru. The single terrestrial species, *Peristeria elata,* is the only member of the genus known to occur in Panama. All the others are South American epiphytes with pendent flower scapes reminiscent of *Acineta.*

1. Peristeria elata Hook. in Bot. Mag. *t. 3116.* 1831.

Erect, stately, terrestrial herbs. Pseudobulbs stout, fleshy, broadly ovoid, subconic or subcylindric, 4–12 cm. long and 4–8 cm. wide, the bases enveloped in several closely imbricating papery bracts, the upper 1–2 of which are foliaceous, the apex of the pseudobulb with 3–5 broadly lanceolate, plicate, acuminate, deciduous leaves 3–10 dm. long and 6–12 cm. wide; the old pseudobulbs often wrinkled, the brown, papery, imbricating, unarmed bases of the fallen leaves persistent and enveloping the apex. Inflorescences tall, solitary, erect, unbranched racemes 8–13 dm. long, produced simultaneously beside the new growth at the base of the pseudobulbs and developing concurrently with it, actual flowering being delayed until the pseudobulb has matured but before the leaves have fallen. Flowers 10–15 or more, relatively large and conspicuous, fleshy, subglobose, waxy white, strongly fragrant, opening in succession from the lowest upward, 2–4 on the raceme open at one time, relatively widely spaced, with long (about 4 cm.) pedicels, usually subtended on the scape by several to many of the developing seed capsules; the unopened buds above the flowers progressively more crowded toward the apex of the scape. Sepals subequal, fleshy, waxy white, broadly concave, the dorsal sepal free, ovate, obtuse, 2.5–3 cm. long and 2–2.5 cm. broad, laterals somewhat connate at the base, ovate or suborbicular, shortly acute, 2.5–3 cm. long and 2.5–3 cm. wide. Petals elliptic-obovate, obtuse, 20–25 mm. long

Fig. 168. *Peristeria elata*

and 15–18 mm. wide. Lip very fleshy, the claw or hypochile broad, continuous with the base of the column, the lateral margins with ascending wings which are white, heavily spotted rose-red, the inner basal surface thickened into a fleshy lobule; apical lobe of the lip, or epichile, white, articulated with the frontal margin of the hypochile, entire, subquadrate, retuse, nearly truncate, with a central glabrous, fleshy, pure white, ventricose or suborbicular crest. Column short, pure white, subconic, semiterete, 9–11 mm. long. Anther pure white, beaked, superficially resembling the head of a bird.

Costa Rica, Panama, Colombia, and Venezuela.

PANAMÁ: hills near Juan Díaz, sea level, *Powell 213;* without definite locality, *Pring s. n.;* llanos east of Panama City near Río Tecúmen, 100 ft., *Allen 5144;* Chorrera llanos, 50 ft., *Allen 5145;* Cerro Campana, rocky outcrops, 2000 ft., *Allen 5071.* COLÓN: Cerro Santa Rita, in grass along roads, 1200 ft., *Dorothy Allen 5138.* COCLÉ: El Valle de Antón, 1800 ft., *Allen 5072.*

This handsome species is the famous "Holy Ghost" or "Dove Orchid," the national flower of the Republic of Panama. The popular names are suggested by the form of the column, its beaked anther and the lateral winged lobes of the basal claw combining to produce within the waxy white flower a figure resembling that of a dove. The plants are found at low to medium elevations in shaded situations on the margins of grasslands and on rocky outcrops in forest, having been in former times very plentiful in the Canal Zone area. Commercial collecting has now made this an increasingly infrequent plant of the more inaccessible parts of the interior.

54. NEOMOOREA Rolfe

NEOMOOREA Rolfe, in Orch. Rev. 12:30. 1904.

Moorea Rolfe, in Gard. Chron. III, 8:7. 1890, non Lem.

Epiphytic herbs with stout ovoid pseudobulbs, the apex with 2 elliptic-lanceolate, acute or shortly acuminate, plicate leaves, the plants resembling a very robust *Stanhopea.* Inflorescences erect or arching racemes from the base of the pseudobulbs. Flowers relatively large and conspicuous. Sepals subequal, free, spreading. Petals subequal to the sepals but narrower at the base. Lip deeply 3-lobed, articulated to the foot of the column, lateral lobes large, spreading, subreniform, midlobe concave, lanceolate-acuminate, basal crest shortly pedicellate, with 2 lateral erect or spreading wings. Column subclavate, semiterete, somewhat arcuate, not winged, produced at the base into a short, broad foot. Anther terminal, incumbent, operculate; pollinia 4, waxy, in 2 unequal pairs.

A rare monotypic genus, previously known only from Colombia.

1. NEOMOOREA IRRORATA Rolfe, in Orch. Rev. 12:30. 1904.

Moorea irrorata Rolfe, in Gard. Chron. III, 8:7. 1890.

Erect epiphytic herbs; the primary roots with many erect, white, spinous secondary rootlets which form a dense mat about the base of the plant. Pseudobulbs stout, ovoid, laterally compressed, furrowed, 4–11 cm. long and 2.5–6 cm. wide, the apex with 2 elliptic-lanceolate, plicate, acute or shortly acuminate, strongly veined, subcoriaceous leaves 45–75 cm. long and 10–13 cm. wide. Inflorescences erect or arching racemes 15–45 cm. long, from the base of the pseudobulbs. Flowers few to about 12, relatively large and conspicuous. Sepals subequal, free, spreading, concave, reddish brown, the bases white, the dorsal sepal elliptic-lanceolate, acute, 2–2.5 cm. long and 1–1.2 cm. wide, laterals elliptic-ovate, acute, 2.2–2.8 cm. long and 1.6–1.8 cm. wide. Petals elliptic-obovate, acute, reddish brown with a white base, 2.2–2.5 cm. long and 1.2–1.4 cm. wide. Lip deeply 3-lobed, articulated to the short column foot, 1.4–1.6 cm. long and 1.5–1.7 cm. wide when spread out, lateral lobes large, spreading, subreniform, pale yellow, banded and marked with brownish purple, mid-lobe concave, lanceolate-acuminate, pale yellow spotted red; basal crest conspicuous, erect, shortly pedicellate, with two lateral, erect, subfalcate wings. Column subclavate, somewhat arcuate, not winged, 12–14 mm. long, the base with a short, broad foot.

Panama and Colombia.

CANAL ZONE (?): exact locality unknown, probably Gatún Lake or the vicinity of Río Trinidad, *Hunter s. n.*

A rare Colombian species known in Panama from a few collections of sterile plants from the vicinity of the Río Trinidad, on Gatún Lake, and a single flowering specimen collected and photographed by Mr. A. A. Hunter.

54-A. POLYCYCNIS Rchb. f.

POLYCYCNIS Rchb. f. in Bonplandia 3:218. 1855; Benth. & Hook. Gen. Pl. 3:553. 1883.

Erect epiphytic herbs, the plants somewhat resembling a *Stanhopea*. Pseudobulbs ovoid or subcylindric, the bases enveloped in sheathing bracts, the apex with 1–3 broadly elliptic-lanceolate, plicate leaves. Inflorescences elongate, arching or pendulous racemes from the base of the pseudobulbs. Flowers numerous, membranaceous, pedicellate, somewhat reminiscent of those of a *Gongora*. Sepals subequal, narrowly elliptic-lanceolate, free, or the laterals connate at the base, spreading or reflexed. Petals subequal to the sepals but narrower, sometimes with an elongate, substipitate base. Lip usually with a 3-lobed basal claw or hypochile which is adnate to the base of the column, the lateral lobes erect or spreading, the apex usually hirsute or pubescent; the base of the epichile inserted on the under-surface of the hypochile well back of the apex, producing the effect in some species of a double lip; epichile entire or obscurely 3-lobed, subcordate, obovate or lanceolate, obtuse, acute or acuminate, lateral lobes, if present, subauriculate and spreading; disk often hirsute or pubescent. Column slender, footless, elongate, arcuate, terete below, dilated and truncate above. Anther terminal, operculate, incumbent, 1-celled; pollinia 2, waxy.

Fig. 169. *Polycycnis barbata*

About 7 species of American epiphytic herbs, ranging from Costa Rica to Brazil and Peru, only one being thus far known from Panama. *Polycycnis gratiosa* Rchb. f., from adjacent Costa Rica, seems to differ from our species only in the somewhat smaller flowers and the subfalcate, rather than obtuse, lateral auricles of the hypochile, characters scarcely warranting specific segregation. For the purposes of this treatment they are considered as being identical.

1. POLYCYCNIS BARBATA (Lindl.) Rchb. f. in Bonplandia 3:218. 1855.

Cycnoches barbatum Lindl. in Jour. Hort. Soc. Lond. 4:268. 1849.
Polycycnis gratiosa Endres & Rchb. f. in Gard. Chron. 1451. 1871.

Epiphytic herbs with ovoid, ridged pseudobulbs 2.5–4.5 cm. long and 1.8–2.5 cm. wide, bearing at the apex a single elliptic-lanceolate, plicate, acute or acuminate leaf 25–40 cm. long and 4–10 cm. wide. Inflorescences arching or pendent racemes 28–32 cm. long, from the base of the pseudobulbs, the rachis minutely pubescent. Flowers many, membranaceous, relatively large, on elongate pubescent pedicels. Sepals subequal, spreading or reflexed, concave, pale translucent yellow spotted red, the dorsal sepal free, lanceolate-acuminate, 17–25 mm. long and 6–8 mm. wide when spread out, laterals somewhat obliquely lanceolate, acuminate, connate at the base, 18–24 mm. long and 6–8 mm. wide. Petals narrowly oblanceolate, with slender substipitate bases, pale translucent yellow spotted red, 18–24 mm. long and 2.5–3 mm. wide. Lip with a 3-lobed basal claw or hypochile adnate to the base of the column, white spotted red, 7–9 mm. long, the lateral lobes auriculate-obtuse or subfalcate, acute, erect; the apex of the hypochile with a central, densely pubescent, carinate projection; epichile obscurely 3-lobed, white spotted purple, ovate, acuminate, lateral lobes subauriculate and spreading; the base of the epichile inserted about midway on the under-surface of the hypochile, producing the effect of a double lip, one slightly above and behind the other; disk densely pubescent. Column slender, green, footless, arcuate, terete below, dilated and truncate above, 1.8–2.2 cm. long. Anther purple.

Costa Rica, Panama, Colombia, Venezuela, and Brazil.

COCLÉ: crest of Cerro Pajita, hills north of El Valle de Antón, 3600 ft., *Allen 4314*.

55. STANHOPEA Frost ex Hook.

STANHOPEA Frost ex Hook. in Bot. Mag. *t. 2948, 2949.* 1829; Benth. & Hook. Gen. Pl. 3:549. 1883.

Ceratochilus Lindl. in Lodd. Bot. Cab. 15: *t. 1414.* 1828, non Blume.
Stanhopeastrum Rchb. f. in Bot. Zeit. 10:927. 1852.

Epiphytic herbs with ovoid or subcylindric, more or less ridged pseudobulbs, the apex with a single broad, petiolate, plicate, strongly veined, elliptic-lanceolate leaf. Inflorescences short, pendulous racemes from the base of the pseudobulbs, the rachis enveloped in several broad, papery, imbricating bracts. Flowers usually

large, conspicuous, 2 to about 9, on long pedicels, each shielded by a broad, papery, spathaceous bract. The genus is divided into two very distinct sections, Ecornuta and Eustanhopea, based on the structure of the lip. In both sections sepals membranaceous and concave, the dorsal sepal free and erect, the laterals broader, reflexed and connate at the base. Petals membranaceous, subequal to the dorsal sepal, but usually narrower, with undulate margins. In Ecornuta: lip essentially simple and undivided, adnate to the base of the column, with an inflated, very fleshy, saccate or calceiform, basal claw or hypochile, surmounted by a much-reduced and confluent apical lobe. In Eustanhopea: fleshy lip complexly 2- or 3-parted, inserted on the base of the column, usually divided into a subsaccate or cymbiform, basal claw or hypochile, with or without short, broad teeth on the inner margins of the basal concavity; a short mid-section or mesochile sometimes simple but more frequently with short or elongate, usually falcately incurved, acuminate, lateral horns, and an apical lobe or epichile which usually is articulated to the apex of the mesochile, entire and spreading, or 3-lobed and variously shaped. In both sections column elongate, somewhat arcuate, with or without broad lateral wings. Anther terminal, operculate, incumbent, 1-celled; pollinia 2, waxy.

A remarkable genus mostly of large-flowered American epiphytes, ranging from southern Mexico to Peru and Brazil. Many species have been described, often based on inadequate dried material or isolated specimens flowering in European greenhouses. Undoubtedly comparison of type material would reduce the present inflated list of names to about eight valid species. So far as can be determined from available material, four entities have been found thus far in Panama.

a. Lip simple, undivided (Section Ecornuta) ..... 3. S. pulla
aa. Lip complexly 3-parted (Section Eustanhopea)
  b. Hypochile cymbiform, broadly elliptic-lunate in profile, distinctly longer than broad, the inner margins of the basal concavity entire.... 2. S. oculata
  bb. Hypochile inflated, saccate or subsaccate, geniculate or broadly obovate in profile, about as long as broad, or scarcely longer, the inner margins of the basal concavity with short, broad teeth.
    c. Hypochile in profile geniculate, somewhat longer than broad, the apex oblique, the lateral margins of the canal closely appressed..... 4. S. Wardii
    cc. Hypochile in profile obovate, not geniculate, about as broad as long, the apex abruptly truncate and concave, the lateral margins of the canal spreading ..... 1. S. graveolens

1. Stanhopea graveolens Lindl. in Bot. Reg. n. s. 3: Misc. 59. 1840.

Stanhopea Warscewicziana Kl. in Allgem. Gartenzeit. 20:214. 1852.
Stanhopea inodora Rchb. f. Xenia Orch. 1:121. 1858, non Lodd.
Stanhopea costaricensis Rchb. f. in Hamb. Gartenzeit. 16:424. 1860.
Stanhopea oculata var. *constricta* Klinge. in Acta Hort. Petropol. 17:15, *t. 3, fig. 26–27.* 1898.

Erect epiphytic herbs, with ovoid, ridged, subconic pseudobulbs 2.5–4 cm. long and 2–3 cm. wide, the apex with a single firm, lanceolate to elliptic-lanceolate,

plicate, acute leaf 28–60 cm. long and 7–11 cm. wide. Inflorescences short, pendulous, from the base of the pseudobulbs, the rachis enveloped in several papery, spathaceous bracts. Flowers large and conspicuous, very fragrant, white, pale yellow, or yellow with reddish brown or purple dots, the sepals and petals often with more or less circular rings, the base of the hypochile with or without 2 lateral dark purple "eyes" or blotches. Sepals membranaceous, the dorsal sepal free, erect, concave, lanceolate, acute, 6–7.5 cm. long and 1.4–1.6 cm. wide, laterals reflexed, connate at the base, elliptic-lanceolate, acute, 6–7.5 cm. long and 2–3 cm. broad. Petals membranaceous, reflexed, with undulate margins, lanceolate, acute or acuminate, 4.5–5.5 cm. long and 1.0–1.8 cm. wide. Lip fleshy, complexly 3-parted, 5–6 cm. long, the hypochile broadly inflated, obovate in profile, not geniculate, abruptly truncate and concave at the apex, about as broad as long, the lateral margins with broadly falcate thickenings, the canal to the basal concavity ample, the margins not closely appressed; mesochile short, inserted on the concave apex of the hypochile, the lateral margins with 2 elongate, falcate, acuminate, incurved horns; epichile articulated with the apex of the mesochile, elliptic-ovate, acute or apiculate, with more or less reflexed margins. Column elongate, arcuate, terete below, the apical half broadly winged, 4.5–6 cm. long.

Mexico, Costa Rica, Panama, and Brazil, and probably adjacent areas.

PANAMÁ: hills east of city, near San Juan, sea level, *Powell 295;* McComber Hill, sea level, *Powell 302;* Cerro Campana, 2000 ft., *Allen 4557.* CANAL ZONE: Pedro Miguel, sea level, *Powell 303.*

This species has previously been known in Panama under the name of *Stanhopea Bucephalus*, but unfortunately this must now be listed as a synonym of *S. oculata.* The plants within our area seem for the most part to be confined to the lowlands of both coasts. The fragrant flowers are variable in color, and usually are produced in May and June, lasting only two or three days.

2. STANHOPEA OCULATA (Lodd.) Lindl. Gen. & Spec. Orch. Pl. 158. 1832, as to basinym, but not as to plant described.

Ceratochilus oculatus Lodd. Bot. Cab. 18: *t. 1764.* 1831.
Stanhopea Bucephalus Lindl. Gen. & Sp. Orch. Pl. 157. 1832.

Epiphytic herbs with short, ovoid, subconic pseudobulbs bearing at the apex a single broad, plicate, petiolate, subcoriaceous, elliptic-lanceolate, acute leaf 35–50 cm. long and 8–12 cm. wide. Inflorescences short pendulous racemes typical of the genus. Flowers 2–4, large, creamy white (in our specimens). Sepals membranaceous, the dorsal sepal free, erect, elliptic-lanceolate, concave, acute, 6.5–7.5 cm. long and 1.8–3.5 cm. wide, laterals somewhat connate at the base, reflexed, rather obliquely elliptic-lanceolate, acute, 6–7.5 cm. long and 2–3.5 cm. wide. Petals membranaceous, reflexed, linear-lanceolate, acuminate, 5–6.5 cm. long and 1.1–1.5 cm. wide. Lip fleshy, elongate, 4.5–6.5 cm. long; the hypochile cymbiform, deeply concave, with slender, elongate, falcate thickenings on the lateral

margins, in profile broadly elliptic-lunate, about twice as long as broad (in fresh material), or slightly undulate and about 4 times as long as broad (in dried material), the margins of the canal to the basal concavity closely appressed; the mesochile short, inserted on the apex of the hypochile, with 2 lateral, slender, falcate, incurved, elongate horns; the epichile articulated with the apex of the mesochile, obovate, abruptly apiculate. Column elongate, arcuate, semiterete below, broadly winged above, 5–6.5 cm. long.

Mexico and Panama, and probably adjacent Central and South America.

COCLÉ: region north of El Valle de Antón, 1000 m., *Fairchild s. n., Allen 2931.*

This very striking and handsome species has been found thus far in our area only in the wet highland forests north of El Valle de Antón, in Coclé Province, where the plants seem to be confined to the tops of the tallest trees. The flowers in our specimens were produced in June, being unusually large, and pure creamy white. There seems to be no doubt that the present confusion of names has in considerable part arisen from the unfortunate circumstance that Lindley, while transfering *Ceratochilus oculatus* Lodd. (Bot. Cab. *t. 1764.* 1831) to the genus *Stanhopea,* in his accompanying description (Gen. & Spec. Orch. Pl. 158. 1832) actually gave the basic characters of the then undetected *Stanhopea Wardii,* and also (*ibid.* 157. 1832) re-described the Loddiges plant under the name of *Stanhopea Bucephalus.*

3. STANHOPEA PULLA Rchb. f. in Gard. Chron. n. s. 7:810. 1877.

Erect epiphytic herbs. Pseudobulbs short, stout, ovoid, subconic, somewhat wrinkled, often nearly black, 2.5–3.5 cm. long and 2–2.5 cm. wide, enveloped in 3–4 fibrous, brown, papery bracts, the apex with a single elliptic-lanceolate, long-petiolate, plicate, acute or acuminate leaf 40–60 cm. long and 7–10 cm. wide. Inflorescences very short, pendent, produced from the base of the pseudobulbs, the rachis enveloped in several closely imbricating papery bracts, the apical 2–3 of which are expanded and spathaceous, 3–3.5 cm. long and 1.5–2.0 cm. broad, arching over the flowers. Flowers the smallest known for the genus, usually 2, which face each other on the scape. Sepals membranaceous, pale yellow, concave, the dorsal sepal free, erect, elliptic-lanceolate, acute, 20–30 mm. long and 10–20 mm. wide when spread out; laterals connate at the base, reflexed, ovate to broadly subfalcate, acute, 2.5–3.5 cm. long and 1.5–2.5 cm. broad. Petals membranaceous, reflexed, yellow, ligular, abruptly acute, 2–3 cm. long and .8–1.2 cm. wide. Lip very fleshy, waxy, simple, undivided, tan marked and margined with red-brown, the body composed of the hypochile, which is broadly inflated at the base and adnate to the base of the column, 18–25 mm. long and 18–20 mm. broad, lateral margins more or less erect, the ventral surface of the apex of the hypochile broadly concave; the inner disk with an elongate, more or less prominent, central, reddish-brown keel, terminating at the apex in a short, subcordate acute, fleshy boss confluent with the apex of the hypochile. Column somewhat arcuate, 1.8–2 cm. long, semiterete, without broad lateral wings.

Fig. 170. *Stanhopea Wardii*

Costa Rica and Panama.

CANAL ZONE: vic. Gatún, sea level, *Butcher s. n.* COCLÉ: El Valle de Antón, 800 m., *Cope s. n.* VERAGUAS: Cerro Tuté, region west of Santa Fé, 2500–3000 ft., *Fairchild s. n.*, *Allen 4507, 5200.*

Apparently a frequent species, to be expected in areas of low to moderate elevation of the Atlantic slope and adjacent high-rainfall portions of the Pacific watershed. Thus far, the species seems to be most frequent in the mountains west of Santa Fé, in Veraguas Province. The flowers are quite variable in size and to a lesser degree in structure.

4. STANHOPEA WARDII Lodd. ex Lindl. Sert. Orch. *t. 20.* 1838.

Stanhopea aurea Lodd. ex Lindl. in Bot. Reg. n. s. 4: Misc. 11. 1841.
Stanhopea venusta Lindl. loc. cit. 1841.
Stanhopea amoena Kl. in Allgem. Gartenzeit. 20:273. 1852.

Erect epiphytic herbs, the plants nearly identical with those of *Stanhopea graveolens*. Pseudobulbs short, ovoid, the apex with a single broad plicate, petiolate leaf. Flowers relatively large, on short or somewhat elongate, pendent racemes from the base of the pseudobulbs. Sepals membranaceous, concave, pale yellow dotted brownish purple, the dorsal sepal free, erect, elliptic-lanceolate, acute or apiculate, 4.5–6 cm. long and 1.5–2.5 cm. wide, laterals somewhat connate at the base, reflexed, elliptic-lanceolate, acute, 4.5–6 cm. long and 2–3 cm. wide. Petals pale yellow, dotted brownish purple, reflexed, with undulate margins, lanceolate-acuminate, 4–5 cm. long and .8–1.5 cm. wide. Lip very fleshy, complexly 3-parted, 4.5–5 cm. long; the hypochile inflated, subsaccate, inserted on the base of the column, with 2 large, lateral, purple-brown spots, in profile geniculate or subgeniculate, with (in fresh material) a deeply emarginate, central constriction (in fresh material somewhat longer than broad, in dried material about twice as long as broad), with a more or less pronounced gibbose swelling about the middle of the lower surface; the lateral margins with falcate, acuminate thickenings the bases of which, above the basal concavity, are produced into two short, broad, rather obscure teeth; mesochile short, pale yellow, inserted on the apex of the hypochile, with 2 elongate, acuminate, incurved, falcate horns; epichile pale yellow, articulated to the apex of the mesochile, ovate, acute, concave, with somewhat reflexed margins. Column somewhat arcuate, subterete below, broadly winged above, 4–4.5 cm. long.

Mexico, Guatemala, Costa Rica, Panama, and probably also adjacent areas in Central and South America.

COCLÉ: El Valle Chiquito, 1800 ft., *Allen 5123;* Río Mata Ahogado, 1500 ft., *Allen 5070;* El Valle de Antón, 2000 ft., *Fairchild s. n.* CHIRIQUÍ: without definite locality, 4000 ft., *Powell 103.*

A common, attractive species, closely allied to *Stanhopea oculata*, found in Panama throughout the intermediate highlands of the Pacific slope. The fragrant flowers usually are produced in August and September, lasting about two or three days.

56. GONGORA Ruiz & Pavon

GONGORA Ruiz & Pavon, Fl. Peruv. & Chil. Prodr. 117, *t. 25*. 1794; Benth. & Hook. Gen. Pl. 3:549. 1883; Pfitz. in Engler & Prantl, Pflanzenfam. 2:169. 1888.

Acropera Lindl. Gen. & Sp. Orch. Pl. 172. 1833.

Epiphytic herbs. Pseudobulbs stout, ovoid, ridged, the bases enveloped in 2–3 fibrous, imbricating bracts, the apex with 2–3 broad, plicate, petiolate, elliptic-lanceolate leaves. Inflorescences usually elongate, pendent racemes from the base of the pseudobulbs. Flowers few to many, relatively large, on long pedicels. The genus has been divided by Pfitzer into the two sections ACROPERA and EUGONGORA. In section ACROPERA: pedicels usually strongly arcuate; the lateral sepals about as broad as long, spreading or somewhat reflexed, the apex broadly acute or obtuse and abruptly apiculate; the sepals and petals all more or less connivent at the base; the lip with a narrow, short or elongate, ligular basal claw; the mesochile conspicuously lobed or inflated and saccate, rarely with apical horns or antennae; the epichile elongate, lanceolate-acuminate, sometimes reduced to an obscure apicule, or divided and biligular at the apex; column slender and somewhat arcuate, dilated at the apex, sometimes narrowly winged and obscurely 2-cornute, produced at the base into a foot. In section EUGONGORA: pedicels usually straight or slightly curved; the lateral sepals usually nearly twice as long as broad, strongly reflexed, the apex acuminate, the margins strongly reflexed, the bases inserted on the foot of the column; the dorsal sepal and the petals inserted on the upper column, their bases not connivent with those of the lateral sepals; the lip very fleshy, often laterally compressed, complexly 2-parted, with both a well developed hypochile and epichile; the base of the hypochile with or without short, lateral, rounded, ligular or auriculate callosities, the apical margin usually with 2 slender, erect antennae; the epichile usually with a gibbose or conical, basal projection above the basal constriction; column slender and somewhat arcuate, semiterete below, dilated above, without lateral wings, but with the inserted petals resembling stelidia; the base of the column produced into a foot. In both sections of the genus the anther is terminal, operculate, incumbent, 1-celled or imperfectly 2-celled; pollinia 2, waxy.

A perplexing genus of American epiphytes ranging from southern Mexico to Peru and Brazil. The flowers are of exceedingly complex structure, in many cases almost impossible to describe, yet all too often type descriptions are unaccompanied by figures or if the figures are given they prove to be inadequate in one or several

critical details. Of the many published names, perhaps about a dozen fairly well-marked entities can be segregated, but even these often are subject to a considerable amount of variation. The treatment of variants of this type is a matter of individual opinion, past practice usually having been to regard them as distinct species which appear in the literature as of equal value. The principal objection to such a method is that it does nothing to express the often very apparent relationships of many of these so-called species to each other. Many groups of entities are found to be identical in nearly every major detail, often having, shall we say, a strong "family" resemblance, and differing only in the absence or presence or development of some one or two structural details. It would seem the obvious course to accentuate these similarities, rather than to obscure them. For the purposes of this treatment, it is proposed therefore to treat these relatively less important deviations from established types as varieties. On this basis, two species, and three well-marked varieties thus far have been found in Panama.

a. Bases of all 3 sepals connivent (Section ACROPERA)
  b. Apex of the mesochile with 2 short lateral horns ..... 2. G. ARMENIACA var. BICORNUTA
  bb. Apex of the mesochile without 2 short lateral horns ..... 1. G. ARMENIACA
aa. Base of the dorsal sepal inserted on the upper column, not connivent with the bases of the lateral sepals (Section EUGONGORA).
  b. Hypochile when seen from above relatively narrow, the base with lateral ligular projections ..... 3. G. MACULATA
  bb. Hypochile when seen from above relatively broad, the base auriculate or with short lateral fleshy rounded horns.
    c. Basal callosities of the hypochile auriculate ..... 4. G. MACULATA var. LATIBASIS
    cc. Basal callosities of the hypochile short, fleshy, rounded horns ..... 5. G. MACULATA var. TRICOLOR

1. GONGORA ARMENIACA (Lindl.) Rchb. f. Xenia Orch. 1:52. 1854.

Acropera armeniaca Lindl. & Paxt. in Paxton's Flow. Gard. 1:94. 1850–51.
Acropera cornuta Kl. in Allgem. Gartenzeit. 20:186. 1852.

Erect epiphytic herbs. Pseudobulbs ovoid, ridged, often somewhat laterally compressed, 2–4.5 cm. long and 1.5–2.5 cm. wide, the bases enveloped in 2–3 papery, imbricating bracts, the apex with 2 elliptic-lanceolate, plicate, acuminate leaves 10–22 cm. long and 2–4.5 cm. wide. Inflorescences more or less elongate, pendent racemes from the base of the pseudobulbs. Flowers usually many, somewhat variable in structure, relatively large and conspicuous. Sepals membranaceous, the bases all connivent, yellow, orange, or salmon, sometimes with purple-brown spots, dorsal sepal erect, concave, elliptic-oblong and acute to broadly rectangular and obtuse or shortly apiculate, 12–18 mm. long and 6–12 mm. wide, laterals spreading or reflexed, their bases inserted on the column foot, obliquely ovate, acute or obtuse and shortly apiculate, 15–17 mm. long and 12–14 mm. broad. Petals membranaceous, pale salmon or orange, lanceolate and abruptly acuminate, or subfalcate and acuminate, 4–6 mm. long and 2.5–3 mm. wide, the attenuate apices usually recurved, the bases broadly spreading and connivent with

Fig. 171 *Gongora armeniaca* var. *bicornuta*

those of the sepals. Lip with a short, ligular basal claw, apparently articulated with the column foot, the central portion or mesochile inflated, subcalceiform, waxy yellow, 8–12 mm. long, the apex broadly obtuse, with a short or elongate, erect, linear-lanceolate, acuminate projection 6–10 mm. long. Column erect, semi-terete below, dilated and subclavate above, 9–11 mm. long, the base produced into a foot. Rostellum conspicuously elongate.

Nicaragua, Costa Rica, and Panama.

CHIRIQUÍ: without definite locality, 4500 ft., *Powell 432*.

2. GONGORA ARMENIACA (Lindl.) Rchb. f. var. BICORNUTA C. Schweinf. & P. H. Allen, in Bot. Mus. Leafl. Harv. Univ. 13:139. 1948.

Plants typical of the species. Sepals pale cream-yellow, densely and minutely spotted red. Petals rich dark red. Lip elongate-calceiform, waxy orange, the dorsal surface with a short, erect, acute lobe near the conjunction of the broad posterior margins, the apex with 2 short, lateral, fleshy horns from between which is produced an elongate, acuminate, erect, orange projection with a rich dark red tip. Column erect, subligular below, dilated above, the apex obscurely winged, with two short pointed horns on either side of the conspicuously elongate rostellum.

Panama.

VERAGUAS: Cerro Tuté, region west of Santa Fé, 3000 ft., *Allen 4648*.

A well-marked variety differing from the type in the presence of 2 fleshy horns on the apex of the mesochile, on either side of the slender central acuminate projection, the short pointed horns on either side of the rostellum at the apex of the column, and in the apparently richer coloring of the floral parts.

3. GONGORA MACULATA Lindl. in Bot. Reg. n. s. 6:196, *t. 1616*. 1833.

Gongora nigrita Lindl. loc. cit. Misc. n. s. 2:59. 1839.
Gongora leucochila Lem. in Fl. des Serres 1:207, *t. 37*. 1845.
Gongora odoratissima Lem. loc. cit. 2:229. 1847.
Gongora retrorsa Rchb. f. in Bonplandia 2:19. 1854.
Gongora Boothiana Hort. ex Rchb. f. Xenia Orch. 1:54. 1854.
Gongora Jenischii Hort. loc. cit. 1854.
Gongora quadricornis Hort. loc. cit. 1854.
Gongora Shepherdii Hort. loc. cit. 1854.
Gongora vitellina Hort. loc. cit. 1854.
Gongora superflua Rchb. f. loc. cit. 2:169. 1873.
Gongora truncata var. *alba* Nash, in Addisonia 2: *t. 46*. 1917.
Gongora Powellii Schltr. in Fedde, Rep. Sp. Nov. Beih. 17:62. 1922.
Gongora unicolor Schltr. loc. cit. 19:229. 1923.

Epiphytic herbs. Pseudobulbs erect, clustered, ovoid, strongly ridged and sulcate, 4.5–6.5 cm. long and 2–3.5 cm. wide, the bases enveloped in 2–3 fibrous, imbricating bracts, the apex with 2-3 lanceolate or elliptic-lanceolate, plicate, acute or acuminate leaves 25–40 cm. long and 5–11 cm. broad. Inflorescences

Fig. 172. *Gongora maculata*

elongate, pendulous racemes from the base of the pseudobulbs. Flowers many, grotesque, strongly fragrant, relatively large, on elongate, slender, nearly straight pedicels. Sepals membranaceous, pale yellow, spotted or banded reddish brown (in our specimens), dorsal sepal free, erect, the base inserted about midway on the column, lanceolate, acuminate, the margins often strongly recurved, 1.5–1.8 cm. long and .4–.6 cm. wide, the base not connivent with the bases of the lateral sepals, lateral sepals strongly reflexed, inserted on the column foot, obliquely ovate, acuminate when spread out, the lateral margins strongly recurved, 20–25 mm. long and 9–14 mm. wide. Petals colored similarly to the sepals, resembling stelidia, the bases inserted on the column and connivent with the base of the dorsal sepal, linear-lanceolate, acuminate, the attenuate apices somewhat recurved, 6–8 mm. long and 1–2 mm. broad. Lip fleshy, 1.5–2 cm. long, pale yellow, marked reddish brown (in our specimens), complexly 2-parted, the short, ligular, basal claw apparently articulated with the column foot; the hypochile saccate, of 2 complex, erect, lateral lobes, the upper closely appressed margins of which combine to form a dorsal keel, the hypochile when seen from above with 2 slender, lateral, ligular, somewhat recurved projections from the base, the apex in profile abruptly truncate and deeply concave, with two lateral erect elongate antennae prolonged into short acuminate teeth; the epichile laterally compressed, about as long as the hypochile, subsaccate and gibbose above the basal constriction, the apex in profile cuneate, with an attenuate recurved tip. Column erect, somewhat arcuate, 15–20 mm. long, terete below, somewhat dilated and subclavate above the point of insertion of the dorsal sepal and petals.

Mexico, British Honduras to Brazil and Ecuador.

CANAL ZONE: Mojinga Swamp, near the mouth of the Río Chagres, sea level, *Allen 870;* Ancon, in hospital grounds, sea level, *Pittier 6627, 6630.* PANAMÁ: Matías Hernández, east of Panama City, sea level, *Pittier 6630;* hills east of Panama City, sea level, *Powell 63, 70, 76, 176.* COLÓN: forests along the Río Boquerón, above the Peluca Hydrographic Station, 90 m., *Hunter & Allen 649* (in part). COCLÉ: El Valle de Antón, 500–700 m., *Hunter & Allen 352;* El Valle Chiquito, 600 m., *Dunn s. n.;* region north of El Valle de Antón, 800 m., *Allen 2943;* mountains beyond La Pintada, 400–600 m., *Hunter & Allen 647.* BOCAS DEL TORO: Water Valley, vic. Chiriquí Lagoon, *von Wedel 1472.*

This common and widely distributed species is found in damp shaded locations at low to moderate elevations throughout our range. It seems possible that this may be the species described by Ruiz & Pavon as *Gongora quinquenervis*, but their description is obscure and entirely inadequate, and a photograph of the type shows it to have been based on fruiting material only; hence it has been considered best to adopt the next available name. As would be expected in a species having such a tremendous geographic range, the flowers in other areas are variable in color and to a lesser degree in size. In Panama, the flowering season is from November to May, individual plants usually producing two or more successive inflorescences.

4 GONGORA MACULATA Lindl. var. LATIBASIS C. Schweinf. & Allen, in Bot. Mus. Leafl. Harv. Univ. 13:144. 1948.

Vegetative material not seen. Pseudobulbs described as round and deeply grooved, about 5 cm. wide, the apex with 2 grayish green leaves 30 cm. long and 10 cm. wide. Sepals membranaceous, dark blood-red, the dorsal sepal erect, inserted on the column, elliptic-lanceolate, acute, 2–2.2 cm. long and 1.2–1.4 cm. broad, the lateral sepals inserted on the column foot, strongly reflexed, obliquely ovate, shortly acuminate, the lateral margins strongly recurved, about 3 cm. long and 2 cm. broad when spread out. Petals inserted on the column, their bases connivent with the base of the dorsal sepal, light green spotted red, linear-lanceolate, acuminate, subfalcate, the attenuate apices incurved, 12–14 mm. long and about 2 mm. broad. Lip very fleshy, complexly 2-parted, dark blood-red; the hypochile when seen from above about 2 cm. long and 1.3 cm. broad at the abruptly truncate base, the lateral lobes broadly auriculate; the apex of the hypochile, seen in profile, with 2 erect, slender antennae prolonged below as short, acute teeth; the epichile typical of the species, except for the basal projection, which in this case is prolonged into an almost conical spur.

Panama.

COLÓN: about 2 miles west of Gatún Dam, 600 ft., *Butcher s. n.*

A very striking and well-marked variety, differing from the type in the larger, more richly colored flowers, the broader, auriculate base of the hypochile, and the prolonged subconic projection at the base of the epichile.

5. GONGORA MACULATA Lindl. var. TRICOLOR Lindl. in Bot. Reg. n. s. 10: *t. 69.* 1847.

Gongora fulva Lindl. loc. cit. 2: *t. 51.* 1839.
Gongora bufonia Lindl. loc. cit. 4: *t. 2.* 1841.

Plants identical with those of the type. Sepals rich yellow to orange, usually spotted or blotched dark red or dark purple. Petals greenish yellow, usually spotted or marked dark red. Lip very fleshy, complexly 2-parted, rich yellow or orange, usually marked dark red, or dark purple. The hypochile when seen from above with a relatively broad base, with two short, fleshy, rounded horns on each side, otherwise identical with the type.

Panama and Peru, and probably adjacent territory.

CANAL ZONE: Mojinga Swamp, near the mouth of the Río Chagres, sea level, *Allen 911.* PANAMÁ: foothills east of Panama City, sea level, *Powell 32, 69, 71, 93.* COLÓN: forests along the Río Boquerón, above the Peluca Hydrographic Station, about 90 m., *Hunter & Allen 649* (in part), *650.* COCLÉ: El Valle de Antón, 1800 ft., *Fairchild s. n.*

Distinguished from the type by the somewhat larger, more richly colored flowers, the somewhat broader base of the hypochile, and the rounded, fleshy, basal horns.

57. CORYANTHES Hook.

Coryanthes Hook. in Bot. Mag. *t. 3102.* 1831; Benth. & Hook. Gen. Pl. 3:549. 1883; Schltr. in Orchis 10:67–82. 1916.

Meliclis Raf. Fl. Tellur. 2:99. 1836.
Panstrepis Raf. loc. cit. 4:41. 1836.
Corynanthes Schlecht. in Bot. Zeit. 6:65. 1848.
Corythantes Lem. in d'Orbigny, Dict. Hist. Nat. 4:259. 1849.

Erect epiphytic herbs. Pseudobulbs slender, subcylindric, tapering, conspicuously ridged, the apex with 2 or rarely 3 lanceolate or elliptic-lanceolate, plicate, strongly veined, subcoriaceous, acute or acuminate leaves. Inflorescences elongate, slender, pendent racemes from the base of the pseudobulbs. Flowers large, fragrant, often brightly colored, usually 2–3, rarely as many as 7, of very complex structure, on slender arching pedicels. The genus has been divided by Schlechter into two sections Eucoryanthes and Lamellunguis. In both sections the sepals broad, membranaceous, free, spreading or strongly reflexed, the margins undulate or recurved, the laterals obliquely subfalcate and much larger than the dorsal sepal; the petals inconspicuous, linear-lanceolate, often subfalcately recurved at the apex, with undulate margins. Lip very fleshy, usually complexly 4-parted, the narrow basal claw continuous with the base of the column; the hypochile spreading and concave, or galeate, glabrous or pubescent; the mesochile more or less elongate and canaliculate. In Eucoryanthes transverse lamellae or excrescences entirely lacking; in Lamellunguis, these conspicuously present. In both sections epichile inflated, very large and galeate or cup-shaped, in nature usually containing a considerable quantity of clear liquid. Column elongate, terete below, without a foot, the base with 2 short, fleshy, often subfalcate horns or glands from which the liquid is excreted, the apex inflexed-clavate and usually shortly 2-alate on either side of the clinandrium. Anther terminal, operculate, incumbent, 2-celled; pollinia 2, waxy.

About 20 species of American epiphytic plants ranging from Guatemala to Peru and Brazil. They usually occur as a conspicuous element in the unique arboreal myrmecophyllous gardens, in the nests of ants of the genera *Camponotus* and *Azteca,* the association often including a purple- or orange-flowered, erect, tufted *Epidendrum* and several apparently specialized succulent-leaved non-orchidaceous plants, among the most frequent being Peperomias and members of the Gesneriaceae. The flowers are probably the most complex and fascinating of the entire Orchidaceae, every detail of the floral structure having been profoundly modified to attract insects and to assure cross-fertilization.

To accomplish insect attraction, the flowers, although lasting only 3–4 days, are usually brightly colored, large, and strongly fragrant, secreting some substance on the inner margins of the epichile which is extremely attractive to hymenopterous insects. The sepals, although large, soon wither, the direction of the insect's

path being left almost entirely to the intricate contrivances of the marvelous labellum. This organ is unique in the Orchidaceae, the apical lobe or epichile resembling an inverted helmet or waxy cup, on one side prolonged below the apex of the column into a short, usually 3-cornute spout-like channel. The column, in its turn, is sharply reflexed at the apex, which rests precisely over the channel, exposing the anther and stigmatic surface to any insect seeking a way out from the interior of the lip.

It would seem that the broad expanse of the mouth of the epichile would provide ample space for an insect to take flight, with only an occasional individual choosing the lateral exit. If the flowers were of longer duration, this might have been left to pure chance, but since time is also an important factor, this possibility of escape by flight has been ingeniously circumvented by the plant in the following manner. Above the cup, on the base of the column, 2 fleshy glands have been developed. When the flowers are fully open and numbers of bees have been attracted to gnaw at the inner margins of the cup, these glands begin secreting a clear liquid, drop by drop, filling the bottom of the cup to the level of the apical channel. Any bee that loses its footing in the competing swarm on the upper margins is precipitated into this liquid, and once its wings have been wet, it has no other choice than to force its way out through the narrow channel below the stigma and anther. Thus the first bee to make the circuit receives the pollinia firmly cemented to its back, to be inserted on the stigma of this or another flower, on the next turn through. A single species of this most remarkable of all orchid genera has thus far been found in Panama.

1. CORYANTHES MACULATA Hook. in Bot. Mag. *t. 3102.* 1831.

Coryanthes maculata Lindl. in Bot. Reg. 21: *t. 1793.* 1835.
Coryanthes Albertinae Karst. Ausw. Neuer Gew. Venez. 5: *t. 1.* 1848.
Coryanthes splendens Barb. Rodr. Gen. & Sp. Orch. Nov. 1:103. 1877.
Coryanthes Hunteriana Schltr. in Fedde Rep. Sp. Nov. Beih. 17:63. 1922.
Coryanthes Powellii Schltr. loc. cit. 64. 1922.

Erect epiphytic herbs with elongate, subcylindric, tapering, strongly ridged pseudobulbs 6.5–15 cm. long and 2.5–4 cm. wide, bearing at the apex 2 firm, lanceolate, plicate, strongly veined, acute or acuminate leaves 30–60 cm. long and 4–10 cm. wide. Inflorescences slender, elongate, pendent racemes 30–50 cm. long, from the base of the pseudobulbs. Flowers usually 2–3, large and attractive, of variable color, the lip complexly 4-parted. Sepals membranaceous, free, clear yellow with a few purple spots, pale purple, or reddish-brown, dorsal sepal suborbicular-ovate, broadly acute and minutely apiculate, the apical half strongly reflexed, the lateral margins revolute, 2–2.5 cm. long and 3–3.5 cm. broad when spread out, lateral sepals very strongly reflexed, from a broadly lobulate base, obliquely subfalcate, or the pair when spread out obliquely dolabriform, 5–6.5 cm. long and 2.5–4 cm. broad. Petals membranaceous, usually colored similarly to the sepals, ligular-lanceolate, the apices obliquely subacute, the margins undulate,

Fig. 173. *Coryanthes maculata*

3–3.5 cm. long and .6–1.0 cm. wide. Lip very fleshy, complexly 4-parted, clear waxy yellow, pale purplish spotted with blood red, or the hypochile yellow, the mesochile and epichile reddish brown on the outer surfaces, the inner epichile white spotted red-brown. Claw of the lip semiterete, continuous with the base of the column; hypochile broadly galeate, glabrous, the apex obtuse or subacute, in profile 2–2.5 cm. long and 2–2.5 cm. broad; mesochile canaliculate, glabrous, the basal half covered by the hypochile, in profile 2.5–3 cm. long and .8–1.5 cm. wide; epichile deeply cucullate or galeate, broadly obtuse, seen in profile 3–3.5 cm. long and 2.5–3.5 cm. broad, in fresh material resembling a waxy cup or bucket, prolonged below the apex of the column into a 3-cornute spout or channel. Column subterete, without a foot, near the base with 2 broad, lateral, subfalcate or obliquely auriculate glands, 8–10 mm. long and 5–10 mm. wide, the apex strongly reflexed and shortly 2-alate on either side of the clinandrium.

Panama, Venezuela, the Guianas, Brazil, and probably other adjacent territory.

CANAL ZONE: Río Indio, near Gatún, sea level, *Butcher s. n.*, *Allen 2054*. PANAMÁ: hills east of Panama City, sea level, *Powell 19, 156, 305*.

In Panama the plants are frequently found in the tops of slender trees, in ants' nests, often associated with *Epidendrum imatophyllum*. They are well protected by the belligerent ants and are painful subjects to collect, and still more painful to transport. Moreover, they seldom thrive in cultivation, possibly from lack of some essential element contributed by the ants in their natural association. It seems possible that this may be only a well-marked variety of *Coryanthes speciosa*.

58. XYLOBIUM Lindl.

XYLOBIUM Lindl. in Bot. Reg. 11: sub *t. 897*. 1825; Benth. & Hook. Gen. Pl. 3:547. 1883.

Onkeripus Raf. Fl. Tellur. 4:42. 1836.
Pentulops Raf. loc. cit. 1836.

Epiphytic herbs with short or elongate, ovoid or semiterete pseudobulbs, the bases enveloped in 2–4 papery, brown, imbricating bracts, the apices with 1–2 lanceolate, plicate, subcoriaceous, strongly veined, acute or acuminate leaves. Inflorescences short or elongate, erect or arching racemes from the base of the pseudobulbs. Flowers few to many, on short pedicels, reminiscent of those of a small-flowered *Maxillaria*. Sepals subequal, membranaceous, spreading, the dorsal sepal free, the laterals broader, adnate to the foot of the column, forming a short mentum, the dorsal surface, particularly near the apex, usually with an erect central keel. Petals membranaceous, subequal to the dorsal sepal. Lip entire or 3-lobed, the lateral lobes or margins erect, the base articulated with the foot of the column; disk smooth, callused or with parallel prominent nerves or lamellae. Column short, erect, somewhat arcuate, semiterete, the apex subclavate or narrowly winged, the base produced into a foot. Anther terminal, operculate, incumbent, 1-celled or imperfectly 2-celled; pollinia 2 or 4, waxy.

About 20 species of American epiphytes, found from southern Mexico to Peru and Brazil, and in the West Indies. The flowers considerably resemble those of some species of *Maxillaria*. However, the genus is amply separated by the racemose flowering habit and the plicate rather than coriaceous leaves. Three species are known from Panama.

a. Lip conspicuously 3-lobed.
  b. Lip densely papillose. Pseudobulbs elongate, semi-terete, diphyllous.... 1. X. ELONGATUM
  bb. Lip not papillose. Pseudobulbs ovoid, stout, di- or triphyllous..... 2. X. FOVEATUM
aa. Lip entire or obscurely 3-lobed. Pseudobulbs short, subcylindric, monophyllous or very rarely diphyllous ..... 3. X. POWELLII

1. XYLOBIUM ELONGATUM (Lindl.) Hemsl. Biol. Centr.-Amer. Bot. 3:252. 1885.

Maxillaria elongata Lindl. & Paxt. in Paxton's Flow. Gard. 3:69, *fig. 264.* 1852–53.

Epiphytic herbs with erect, elongate, semiterete pseudobulbs 10–27 cm. long and .4–1.2 cm. wide, the bases enveloped in 3–4 brown, papery, imbricating bracts, the apices with 2 lanceolate or elliptic-lanceolate, plicate, strongly veined, acute or acuminate leaves 15–36 cm. long and 2.5–9 cm. wide. Inflorescences erect, slender racemes 10–15 cm. long, produced from the base of the pseudobulbs, the lower portion below the flowers enveloped in several broad, papery, closely imbricating bracts. Flowers few to many, comparatively large, on short pedicels. Sepals membranaceous, white or pale yellow, spreading, subequal, the dorsal sepal free, lanceolate, acute or acuminate, 15–25 mm. long and 4–7 mm. broad, lateral sepals adnate at the base to the column foot, forming a short mentum, somewhat obliquely lanceolate, acuminate, with a strong central keel on the dorsal surface, 15–30 mm. long and 4–8 mm. wide. Petals membranaceous, white or pale yellow, spreading, subequal to the dorsal sepal, lanceolate, acuminate, 15–20 mm. long and 4–7 mm. wide. Lip 3-lobed, articulated at the base with the foot of the column, 14–18 mm. long and 4–8 mm. broad, white or pale yellow, with purple or maroon stripes, lateral lobes conspicuous, erect, about equaling the column, apical lobe densely papillose, the lateral margins strongly inflexed; disk with 5 thickened central nerves or lamellae. Column short, stout, terete, produced at the base into a long broad foot. Anther terminal, operculate, incumbent, 1-celled; pollinia 4, waxy.

Costa Rica and Panama.

COCLÉ: hills north of El Valle de Antón, 1000 m., *Allen 2705, 2745, 3739.* CHIRIQUÍ: near Boquete, 3800–4000 ft., *Powell 167;* Bajo Mono-Robalo trail, western slopes of Cerro Horqueta, 5000–7000 ft., *Allen 4787.*

A frequent plant of the highland forests above about 2500 ft., readily distinguished from the other local species by the extremely elongate, slender, diphyllous pseudobulbs, and the densely papillose lip. Usually to be found in damp situations in heavy shade, often on the lower trunks of large trees. The flowering season is during the fall and winter months, from September to March.

2. XYLOBIUM FOVEATUM (Lindl.) Nicholson, Dict. Gard. 4:225. 1887.

Maxillaria foveata Lindl. in Bot. Reg. n. s. 2: Misc. 2. 1839.
Maxillaria concava Lindl. loc. cit. 7: Misc. 4. 1844.
Maxillaria stachybiorum Rchb. f. in Bot. Zeit. 10:735. 1852.
Xylobium concavum Hemsley, Biol. Centr.-Amer. Bot. 3:252. 1883.
Xylobium stachybiorum Hemsley, loc. cit. 1883.
Xylobium Filomenoi Schltr. in Fedde Rep. Sp. Nov. Beih. 9:100. 1921.

Epiphytic herbs. Pseudobulbs stout, ovoid or subconic, tapering, smooth or somewhat ridged, 4–9 cm. long and 1.5–4 cm. wide, the base enveloped in 2–3 brown, fibrous, imbricating bracts, the apex with 2–3, plicate, lanceolate, strongly veined, acute or acuminate, subcoriaceous leaves 24–40 cm. long and 2.5–7 cm. wide, the blades usually deciduous after the second year, the apex of the old pseudobulbs unarmed. Inflorescences erect racemes 12–30 cm. tall, from the base of the pseudobulbs, the lower rachis below the flowers enveloped in several broad, papery bracts. Flowers usually many, fragrant, on short pedicels. Sepals membranaceous, subequal, spreading, creamy white, the dorsal sepal free, lanceolate-acuminate, 10–14 mm. long and 3–4 mm. wide, laterals adnate to the foot of the column, forming a mentum, subfalcately lanceolate-acuminate, 12–14 mm. long and 3–4 mm. wide, the dorsal surface with a prominent central keel. Petals subequal to the dorsal sepal, membranaceous, creamy white, lanceolate-acuminate, 8–10 mm. long and 2–3 mm. wide. Lip creamy white with reddish veining on the disk, conspicuously 3-lobed, 10–12 mm. long, articulated at the base with the foot of the column, the lateral lobes rounded, erect, about equaling or somewhat exceeding the column, apical lobe obtuse, spreading; disk with 5 thickened nerves or keels. Column very short, semiterete, the apex obtuse; the base produced into a long broad foot. Anther 1-celled; pollinia 4.

Mexico to Peru and British Guiana; Jamaica.

CANAL ZONE: Barro Colorado Island, *Aviles 32*. PANAMÁ: Ceiba Tierra, sea level, *Powell 3069;* Ana Lago, sea level, *Powell 3064;* hills east of Panama City, sea level, *Powell 27;* Chiva-Chiva, sea level, *Powell 3053;* vic. Pacora, sea level, *Powell 3026, Allen 821;* forest along telephone cable, vic. Río Indio Hydrographic Station, Upper Madden region, *Steyermark & Allen 17466;* San José Island, Perlas Archipelago, *Johnston 1017, 1117.*

A very frequent species found throughout the lowlands of our area, flowering during the fall and winter months from November to March.

3. XYLOBIUM POWELLII Schltr. in Fedde, Rep. Sp. Nov. Beih. 17:66. 1922.

Xylobium sublobatum Schltr. loc. cit. 19:51. 1923.

Erect epiphytic herbs with slender subterete (rarely cylindric-tapering) pseudobulbs 4–7 cm. long and .7–1.8 cm. wide, enveloped at the base in 2–3 fibrous, imbricating bracts, the apex with 1 (rarely 2) lanceolate, plicate, strongly veined, long-petioled, acute or shortly acuminate leaves 20–60 cm. long and 2–5.5 cm. wide. Inflorescences erect racemes, 9–15 cm. tall, the bases below the flower-

ing portion enveloped in several papery, imbricating bracts. Flowers few to many, on short pedicels, yellow or tan, sometimes tinged with light green. Sepals membranaceous, subequal, spreading, the dorsal sepal elliptic-lanceolate, acute, 10–12 mm. long and 4–6 mm. wide, laterals adnate to the foot of the column, forming a mentum, from an oblique base, lanceolate, acute, 12–14 mm. long and 4–6 mm. wide, the dorsal surface with a prominent central keel. Petals subequal to the dorsal sepal, linear-lanceolate, acute, 10–12 mm. long and 3–4 mm. broad. Lip entire or obscurely 3-lobed, articulated at the base with the column foot, 10–12 mm. long; the narrow lateral lobes, if present, or the margins erect; the apical lobe somewhat concave, subacute; disk with 3 prominent erect nerves or keels. Column very short, subterete, produced at the base into a foot. Anther 1-celled; pollinia 4.

Costa Rica and Panama.

CHIRIQUÍ: without definite locality, 4000 ft., *Powell 117;* valley of the upper Río Chiriquí Viejo, vic. of Monte Lirio, 1300–1900 m., *Seibert 135, 223;* Finca Lérida to Peña Blanca, 1750–2000 m., *Woodson & Schery 325;* Quebrada Velo, 1800 m., *Woodson & Schery 281;* vic. Bajo Mono and Quebrada Chiquero, 1500 m., *Woodson & Schery 534;* Bajo Chorro, 6000 ft., *Davidson 241.*

A very frequent species of the Chiriqui highlands, flowering in July and August. Although the type specimen of *Xylobium Powellii* was described as having two leaves, nearly all plants seen had a single leaf. Type material has not been available for comparison, but our species seems to agree very well with an earlier monophyllous species from Guatemala, *Xylobium Tuerckheimii* Kränzl., and it seems likely that subsequent investigation may prove them to be identical.

59. BIFRENARIA Lindl.

BIFRENARIA Lindl. Gen. & Spec. Orch. Pl. 152. 1833; Benth. & Hook. Gen. Pl. 3:546. 1883.

Adipe Raf. Fl. Tellur. 2:101. 1836.
Stenocoryne Lindl. in Bot. Reg. n. s. 6: Misc. 53. 1843.
Lindleyella Schltr. Die Orchideen, p. 414. 1914.

Epiphytic herbs. Pseudobulbs short, fleshy, ovoid, subconic or subpyramidal, often abruptly 4-angulate or laterally compressed, the bases enveloped in 2–3 fibrous, imbricating bracts, the apex with 1–2 lanceolate or elliptic-lanceolate, plicate, strongly veined, acute or acuminate leaves. There are two quite distinctive groups of species, one of which has been segregated by Schlechter as a separate genus under the name *Lindleyella.* Schweinfurth (Bot. Mus. Leafl. Harv. Univ. 11:246. 1944) has pointed out that the floral characters proposed by Schlechter for such separation are equally applicable to species of the other group, so that it is impossible to accept *Lindleyella* as a valid generic concept. However, since the groups are sufficiently distinctive to be separated on gross characters alone, the name proposed by Schlechter is retained as a section, simply for purposes of convenience. On this basis, those species superficially resembling *Bifrenaria atropurpurea,* the generic type with 1–3 large flowers on short erect racemes, are considered

as representing the section EUBIFRENARIA, while those resembling *Bifrenaria picta* and *B. aurantiaca*, with many small flowers on elongate arching racemes, are considered as representing the section LINDLEYELLA. In both sections of the genus, the sepals are free, subequal, spreading, the laterals adnate to the column foot, forming a short or elongate spur-like mentum. Petals subequal to the dorsal sepal or smaller. Lip 3-lobed, articulated at the base with the foot of the column, lateral lobes erect, the mid-lobe spreading, entire or bifid; disk fleshy, lamellate, denticulate or hirsute. Column erect, thickened, semiterete, wingless, produced at the base into an elongate foot. Anther terminal, operculate, incumbent, strongly convex, sometimes cristate on the dorsal surface, 1-celled or imperfectly 2-celled; pollinia 2 or 4, waxy.

A variable genus of mostly Brazilian epiphytes, a few species ranging to Peru, the Guianas, Trinidad, Venezuela, and Colombia, with a single species of the section LINDLEYELLA known from eastern Panama.

1. BIFRENARIA PICTA (Schltr.) C. Schweinf. in Bot. Mus. Leafl. Harv. Univ. 11:246. 1944.

Lindleyella picta Schltr. in Fedde Rep. Sp. Nov. Beih. 27:173. 1924.

Epiphytic herbs. Pseudobulbs ovoid, laterally compressed, somewhat ridged, 2.5–5 cm. long and 2–2.5 cm. wide, enveloped at the base in 2–3 fibrous imbricating bracts, the apex with a single, long-petiolate, elliptic-lanceolate, plicate, strongly veined, shortly acuminate leaf 38–46 cm. long and 5–6.8 cm. wide. Inflorescences elongate, slender, arching racemes produced from the base of the pseudobulbs. Flowers many, relatively small, on short pedicels, typical of the section LINDLEYELLA. Sepals subequal, spreading, membranaceous, deep red, or red marked with yellow particularly at the base, dorsal sepal free, elliptic-lanceolate, acute, 10–14 mm. long and 3–5 mm. wide, lateral sepals somewhat oblique, elliptic-lanceolate, acute, adnate to the foot of the column, 10–14 mm. long and 4–8 mm. wide. Petals subequal to the dorsal sepal, yellow, spotted red, elliptic-lanceolate, acute, 10–12 mm. long and 4–5 mm. wide. Lip 3-lobed, 10–12 mm. long, red marked with yellow, the base shortly clawed, lateral lobes erect, subfalcate, obliquely obtuse, longer than broad, the anterior margin undulate and crisped; disk between the lateral lobes with a convex, rather obscurely verrucose callus; mid-lobe subreniform or subquadrate, broadly spreading, contracted at the base into an isthmus with a short, suberect, fleshy, obtuse, linguiform callus, the apex obscurely bilobulate, shallowly emarginate, the lateral lobules undulate and crisped. Column semiterete, somewhat arcuate, 6–8 mm. long, produced at the base into a foot. Anther imperfectly 2-celled; pollinia 2, subglobose.

Panama and Colombia.

DARIÉN: Chepigana District, Cana-Cuasi trail, 800 ft., *Terry & Terry 1616.*

The only record for the genus in North America.

60. LYCASTE Lindl.

Lycaste Lindl. in Bot. Reg. Misc. n. s. 6: Misc. 14. 1843; Benth. & Hook. Gen. Pl. 3:547. 1883.

Deppia Raf. Fl. Tellur. 2:51. 1836.

Erect, epiphytic or sometimes pseudo-terrestrial herbs. Pseudobulbs short, fleshy, ovoid or ellipsoid, tapering, often laterally compressed, smooth or plurisulcate, the bases enveloped in several closely imbricating, papery or coarsely fibrous bracts, the upper 1 or 2 of which are usually foliaceous; the apex with 1 to several, usually broad, plicate leaves which are ultimately deciduous, the apex of the old pseudobulbs with or without 2 sharp marginal spines; roots fibrous, often pubescent or conspicuously lanuginose. Inflorescences 1 to many erect, stout or filiform, single-flowered scapes from the base of the pseudobulbs, enveloped in several closely imbricating or distant, tubular or spathaceous, papery bracts. Flowers small to large, usually more or less nodding. Sepals subequal, membranaceous, spreading, the laterals somewhat broader than the dorsal sepal, sometimes somewhat reflexed, adnate at the base to the foot of the column, forming a short mentum. Petals subequal to the dorsal sepal or shorter. Lip conspicuously or obscurely 3-lobed, the base continuous with, or articulated with, the foot of the column, lateral lobes or margins erect, mid-lobe spreading or reflexed; disk with a thickened callus. Column slender, semiterete, rather arcuate, produced at the base into a foot. Anther terminal, operculate, incumbent, 1-celled; pollinia 4, waxy.

A rather perplexing genus of perhaps 25 species of American epiphytes, ranging from southern Mexico to Peru, Brazil, and the West Indies. Although many of the species have been put at one time or another into the allied genus *Maxillaria*, they are readily separable by the plicate, rather than conduplicate leaves. Five species are known to occur in Panama.

a. Apex of the old pseudobulbs armed with 2 conspicuous sharp spines. Flowers produced after the leaves have fallen, or concurrently with the flush of new growth. Pseudobulbs at flowering time without mature foliage.
  b. Lip when spread out about as long as broad; apical lobe without a basal constriction.
    c. Lip more than 1.5 cm. long ..... 1. L. BREVISPATHA
    cc. Lip less than 1.5 cm. long ..... 2. L. CAMPBELLII
  bb. Lip when spread out about twice as long as broad; apical lobe with a basal constriction ..... 5. L. TRICOLOR
aa. Apex of the old pseudobulbs not armed with 2 conspicuous sharp spines. Flowers produced at the end of the current season's growth, after the pseudobulbs have matured, but before the leaves have fallen.
  b. Lip conspicuously 3-lobed, more than twice as long as broad when spread out; apical lobe ovate or subquadrate ..... 3. L. MACROPHYLLA
  bb. Lip obscurely 3-lobed, less than twice as long as broad when spread out; apical lobe broadly obtuse, separated from the laterals by plicate folds ..... 4. L. POWELLII

1. LYCASTE BREVISPATHA Kl. ex Lindl. in Paxton's Flow. Gard. 3:44. 1852–53.

Lycaste candida Lindl. ex Rchb. f. in Walp. Ann. 6:604. 1863.

Epiphytic (rarely pseudo-terrestrial) herbs. Pseudobulbs fleshy, usually elliptic-ovoid, rarely suborbicular, laterally compressed, 4.5–6.5 cm. long and 2–3.5 cm. wide, enveloped at the base in several coarsely fibrous bracts, the apex with 2–4 elliptic-lanceolate, plicate, acute or shortly acuminate leaves which are ultimately deciduous, 15–20 cm. long and 3–5 cm. wide, the apex of the old pseudobulbs armed with 2 conspicuous sharp spines; roots usually conspicuously lanuginose. Inflorescences 1 to many slender, erect scapes 5–7 cm. tall, usually produced concurrently with the flush of new growth from the base of the old leafless pseudobulb, the filiform rachis provided with several distant tubular sheathing bracts, the apical bract usually about half the length of the ovary. Flowers more or less pseudo-campanulate, solitary, somewhat nodding. Sepals subequal, membranaceous, usually pale green to olive-green, rarely rose, the dorsal sepal free, erect, elliptic-lanceolate, acute, the apex strongly recurved, 2.5–2.8 cm. long and 10–15 mm. wide, laterals adnate to the foot of the column, forming a short mentum, from the oblique base elliptic-lanceolate, acute, the apices strongly recurved, 2.5–3 cm. long and 1.0–1.5 cm. wide. Petals subequal to the sepals, white marked rose, or rarely pure white, elliptic-oblanceolate, acute, the apices recurved, 2.4–2.6 cm. long and 1.0–1.5 cm. wide. Lip 3-lobed, articulated at the base with the foot of the column, white with rose markings, or rarely white, nearly as broad as long when spread out, 2.2–2.5 cm. long and 1.8–2.2 cm. wide, lateral lobes erect, rather obscurely emarginate at the subacute apices, mid-lobe broadly obtuse, the apex somewhat reflexed; disk with an elongate, acute, 2-costate linguiform callus. Column semiterete, rather arcuate, 8–9 mm. long, the under-surface conspicuously pubescent, the base produced into a foot.

Costa Rica and Panama.

CHIRIQUÍ: without definite locality, shady places, 4000–4500 ft., *Powell 140;* vic. Finca Lérida, upper forested margins of the Quebrada Velo, 5000 ft., *Allen 4749.*

A fairly frequent species of the Chiriquí highlands, usually being found in shaded places between 4000 and 5000 ft. elevation. The flowers are variable in color, usually being produced from February to about April.

2. LYCASTE CAMPBELLII C. Schweinf. in Johnston, Sargentia 8:103, *fig.* 1949. ined.

Epiphytic herbs with ovoid-ellipsoid, somewhat laterally compressed pseudobulbs 3.5–5 cm. long and 1.5–2.5 cm. wide, enveloped at the base in several coarsely fibrous, imbricating sheaths; apex of the pseudobulbs (during the growing season) with 1–3 plicate, elliptic-lanceolate leaves which are ultimately deciduous, the old pseudobulbs armed at the apex with 2 sharp spines; roots fibrous, lanuginose. Inflorescences 1 to several erect, filiform scapes less than 8 cm. tall, produced from the base of the current pseudobulb after the leaves have fallen. Flowers pseudo-campanulate, more or less nodding, the smallest of the genus in Panama. Sepals

subequal, membranaceous, green, the dorsal sepal ovate-elliptic, acute, about 1.8 cm. long and 1 cm. wide when spread out, laterals adnate to the foot of the column, forming a short conical mentum, from the oblique base oblong-ovate, acute, 1.8 cm. long and about 1 cm. wide. Petals elliptic-ovate, obtuse, abruptly apiculate, yellowish green, about 1.5 cm. long and 1 cm. wide. Lip 3-lobed, contracted at the base and articulated with the foot of the column, yellow, about 1.6 cm. long and .9–1.0 cm. wide when spread out, lateral lobes erect and somewhat incurved, the apices rather obliquely acute, mid-lobe ovate, subacute, with a recurved apicule; disk between the lateral lobes with a concave oblong-obtuse callus. Column short, stout, semiterete, somewhat arcuate, about 6–8 mm. long; obscurely puberulent on the under-surface, produced at the base into a foot.

Panama.

PANAMÁ: San José Island, Perlas Archipelago, high on trees in stream-side forest in area 11-B, *Johnston 1371, Campbell 12.*

Known only from the type collection. Although vegetatively reminiscent of *Lycaste candida* or *L. tricolor*, it may readily be distinguished by the much smaller, differently colored flowers. The season of flowering is given by Dr. Johnston as February.

3. LYCASTE MACROPHYLLA Lindl. in Bot. Reg. n. s. 6: Misc. 14. 1843.

Maxillaria macrophylla Poepp. & Endl. Nov. Gen. & Sp. 1:37, *t. 64.* 1836.
Lycaste plana Lindl. in Bot. Reg. n. s. 5: Misc. 85. 1842.
Lycaste Dowiana Endres & Rchb. f. in Gard. Chron. n. s. 2:194. 1874.
Lycaste Filomenoi Schltr. in Fedde, Rep. Sp. Nov. Beih. 9:100. 1921.

Epiphytic herbs with stout, ovoid, somewhat laterally compressed, often rather angulate or plurisulcate pseudobulbs 4–10 cm. long and 3–6 cm. wide, the bases enveloped in 3–4 closely imbricating, papery bracts, the upper 2 of which are foliaceous, the largest blade about 40 cm. long and 10–12 cm. broad; the apex of the pseudobulbs with 2–3 broad, plicate, oblanceolate, acute or acuminate leaves 40–75 cm. long and 10–12 cm. broad, which are ultimately deciduous; the apices of the old pseudobulbs not armed with sharp spines. Inflorescences few to many erect, single-flowered scapes 8–18 cm. tall, from the base of the mature pseudobulbs, the rachis enveloped in several broad, papery, spathaceous bracts, the uppermost of which is usually broadly cucullate, acute, about equaling or somewhat exceeding the ovary. Flowers large and conspicuous, fragrant, more or less nodding. Sepals subequal, broadly spreading, olive-green, sometimes shaded on the margins with reddish-brown, the dorsal sepal free, erect, lanceolate to elliptic-lanceolate, acute, 4.5–6 cm. long and 1.5–2.5 cm. wide, laterals adnate to the foot of the column, forming a short mentum, from the oblique base lanceolate to elliptic-lanceolate, acute, 4.5–6 cm. long and 2–3 cm. wide. Petals subequal to the sepals, not spreading, more or less parallel with the column, white, often spotted rose-pink, linear-lanceolate to elliptic-oblanceolate, acute, the apices recurved, 4–5 cm. long and 1.8–2.2 cm. broad. Lip 3-lobed, 3–4.5 cm. long and 1.4–1.6 cm. wide when spread out, usually not equaling the petals, narrowed at the base and

articulated with the foot of the column, white, usually with the margins of the apex spotted or blotched rose-red, lateral lobes erect, the apices rather irregularly oblique, mid-lobe spreading, ovate to subquadrate, acute or obtuse, the margins slightly ciliate and incurved; disk with a fleshy, lanceolate, acute, concave callus. Column slender, semiterete, somewhat arcuate, white, 18–23 mm. long.

Costa Rica, Panama, Colombia, Venezuela, Peru, and Bolivia.

COCLÉ: region north of El Valle de Antón, 3000 ft., *Allen 2665, 5067, 5139;* western slope and summit of Cerro Valle Chiquito, 700–800 m., *Seibert 644.* VERAGUAS: forested slopes of Cerro Tuté, west of Santa Fé, 2500–3000 ft., *Allen & Fairchild 4400.* CHIRIQUÍ: without definite locality, 5000 ft., *Powell 246.*

A frequent, rather variable species of the wet highland forests of Coclé, Veraguas, and Chiriquí provinces. The Coclé specimens are rather consistently smaller than those from Veraguas and Chiriquí, particularly in the vegetative parts, but otherwise appear to be very nearly identical. The Coclé form is usually considered as representing *Lycaste Dowiana,* but the supposed differences (shorter floral bract and narrower lip) have been found on careful examination to be inconstant characters, scarcely any two specimens being exactly alike, and, in any event, hardly differences warranting specific segregation. From the evidence now available, the Coclé plants appear to be at most a local form of the widespread and variable *Lycaste macrophylla.* The flowering season is from March to about July.

4. LYCASTE POWELLII Schltr. in Fedde Rep. Sp. Nov. Beih. 17:65. 1922.

Epiphytic, or often pseudo-terrestrial herbs with elliptic-ovoid, laterally compressed, smooth, or somewhat ridged pseudobulbs 3–6 cm. long and 2–3 cm. wide, the bases enveloped in 3–4 papery, closely imbricating bracts the upper 2 of which are usually foliaceous; the apices of the pseudobulbs with 2–3 plicate, lanceolate or elliptic-lanceolate, acute or acuminate, ultimately deciduous leaves 20–35 cm. long and 4–7 cm. broad; the apices of the old pseudobulbs unarmed. Inflorescences 1 to about 4, slender, erect, 1-flowered scapes 5–14 cm. tall, produced from the bases of the mature pseudobulbs before the leaves have fallen, the rachis provided with several distant, papery, tubular, acuminate bracts the uppermost of which is spathaceous and conspicuously exceeds the ovary. Flowers relatively large, very fragrant. Sepals widely spreading, pale translucent green, heavily blotched with chestnut-brown, or wine-red with yellow margins, dorsal sepal free, linear-lanceolate, acute, 3–4 cm. long and .8–1.4 cm. wide, the apex lightly recurved, laterals adnate to the foot of the column, forming a short mentum, from the oblique base, linear-lanceolate, acute, 3–4.2 cm. long and .6–1.4 cm. wide. Petals subequal to the sepals, cream-yellow to nearly white, spotted rose-pink or wine-red, elliptic-lanceolate, obtuse or subacute, 2.5–3.5 cm. long and 1.2–1.8 cm. wide, more or less parallel with the column, the apices strongly reflexed. Lip elliptic-obovate, obtuse or subacute when spread out, 2.6–2.8 cm. long and 1.4–1.7 cm. wide, obscurely 3-lobed, the lateral lobes or margins erect, the mid-lobe short, spreading, obtuse or subacute, separated from the laterals by plicate folds; disk with a short,

fleshy, ligular, obtuse, concave callus. Column semiterete, 1.8–2 cm. long, slightly arcuate, minutely papillose.

Panama.

PANAMÁ: hills east of Panama City, *Powell 15;* Cerro Campana, 2500 ft., *Fairchild s. n.* *COCLÉ: vic. El Valle de Antón, floor and forested ravines in dry hills to the south, 600–800 m., *Allen 761, 2666;* floor of El Valle de Antón, 600 m., *Fairchild s. n.*

A frequent and attractive species of the wooded ravines of the intermediate highlands of Cerro Campana and El Valle de Antón, where they are often found growing on rocks or on low, gnarled trees of the genus *Coccoloba.* The flowering season is usually from July to September.

Fig. 174. *Lycaste tricolor*

5. LYCASTE TRICOLOR (Kl.) Rchb. f. in Walp. Ann. 6:603. 1863.

Maxillaria tricolor Kl. in Allgem. Gartenzeit. 20:186. 1852.
Lycaste Bradeorum Schltr. in Fedde Rep. Sp. Nov. Beih. 19:138. 1923.

Epiphytic herbs with elliptic-ovoid, tapering, laterally compressed, smooth or ridged pseudobulbs 6–9 cm. tall and 2.5–3 cm. wide, the bases enveloped in several coarsely fibrous bracts, the apex (during the growing season) with 3–4 elliptic-lanceolate, plicate, acute or acuminate, deciduous leaves; the apex of the old pseudobulbs armed with 2 short, sharp spines; roots fibrous, lanuginose. Inflorescences 1 to several erect, single-flowered scapes 9–12 cm. tall, from the base of the pseudobulbs, produced after the leaves have fallen or concurrently with the flush of new growth. Flowers pseudo-campanulate, relatively large. Sepals spreading, subequal, the apices strongly recurved, pale green, often spotted with pink, the dorsal sepal free, elliptic-lanceolate, acute, often minutely apiculate, 2.8–3.2 cm. long and 1.2–1.5 cm. wide, lateral sepals adnate at the base to the foot of the column, forming a short mentum, from the oblique base lanceolate, acute, often minutely apiculate, 2.8–3.2 cm. long and 1.0–1.4 cm. wide. Petals subequal to the sepals, spreading, the apices strongly recurved, white, often spotted pink, elliptic-oblanceolate, acute, 2.4–2.6 cm. long and 1.4–1.6 cm. wide. Lip conspicuously 3-lobed, about twice as long as broad when spread out, narrowed at the base and articulated with the foot of the column, white, usually spotted pink, 2.8–3 cm. long and 1.4–1.6 cm. wide when spread out, lateral lobes erect, the anterior margins obscurely emarginate at the obliquely acute apices, mid-lobe subquadrate or ovate, obtuse, with a basal constriction, the apex strongly reflexed; disk with an elongate, acute, concave callus. Column semiterete, somewhat arcuate, 12–14 mm. long, produced at the base into a foot.

Guatemala, Costa Rica, and Panama, and probably adjacent territory.

COCLÉ: Río Mata Ahogado, 1200 ft., *Fairchild s. n.*; Río Mata Ahogado, volcanic badlands southeast of El Valle de Antón, 1500 ft., *Allen 4526*. VERAGUAS: Río Santa María, vic. Santa Fé, 1000 ft., *Allen 4567*.

A frequent and attractive species often found on low-spreading trees overhanging streams in the volcanic badlands of Coclé and Veraguas provinces, usually at about 1000–1500 ft. elevation. It seems possible that subsequent investigation may prove this to be simply a well-marked variety of *Lycaste brevispatha*. The flowering season is in May and June.

60-A. KOELLENSTEINIA Rchb. f.

KOELLENSTEINIA Rchb. f. in Bonplandia 2:17. 1854; Walp. Ann. 6:551. 1863; Schltr. in Orchis 12:24. 1918.

Terrestrial or epiphytic herbs, with or without minute subterete or 4-angulate pseudobulbs. Pseudobulbs when present completely enveloped by the imbricating bases of the foliaceous bracts, the apex with 1 or 2 long-petiolate, slender, plicate

leaves; in plants without pseudobulbs, the several slender, plicate leaves resembling those of a *Bletia*, more or less contracted at the base into a short, sheathing petiole, the basal portions of which are enveloped in several imbricating bracts. Inflorescences lateral, erect, slender racemes, usually more or less equaling the leaves, produced from the base of the current season's growth. Flowers few to many, of moderate size, on short pedicels. Sepals subequal, free, more or less spreading, the laterals usually somewhat broader. Petals subequal to the dorsal sepal or a little less. Lip 3-lobed, contracted at the base into a short claw which is adnate to, or apparently articulated with, the foot of the column, the lateral lobes erect or somewhat spreading, the mid-lobe spreading, rounded or subquadrate, or subreniform, entire, or broadly 2-lobed; disk between the lateral lobes with a thickened callus. Column short, semi-terete, somewhat arcuate, the apical margins projecting and forming a short hood over the clinandrium, the base produced into a short, broad foot. Anther terminal, operculate, incumbent, 1-celled; pollinia 2, waxy.

A South American and West Indian genus previously unrecorded from Panama.

1. KOELLENSTEINIA KELLNERIANA Rchb. f. in Bonplandia 2:17. 1854.

Warrea graveolens Hort. ex Rchb. f. Xenia Orch. 1:65. 1854.

Erect terrestrial herbs, with small, subterete or tetragonous, tapering pseudobulbs 2–3 cm. long and 4–6 mm. wide. Leaves 1 or 2, linear-lanceolate, plicate, acute or acuminate, the bases contracted into a long petiole, 45–70 cm. long and 10–15 mm. wide. Inflorescences erect, 40–60 cm. tall, produced from the base of the current flush of new growth, the peduncle provided with several distant, papery, tubular, acute or acuminate bracts. Flowers of moderate size, few to many, reminiscent of those of a small *Cyrtopodium* or *Warrea*. Sepals rather fleshy, free, subequal, green, the dorsal sepal incurved, rather concave, elliptic-lanceolate, acute, 10–12 mm. long and 4–5 mm. wide, laterals somewhat spreading, rather obliquely elliptic-lanceolate, acute, 10–12 mm. long and 5–6 mm. wide. Petals subequal to the dorsal sepal, submembranaceous, pale green, elliptic-lanceolate, acute, 9–10 mm. long and 3.5–4 mm. wide. Lip rather fleshy, 3-lobed, white transversely barred lavender or purple, 6–8 mm. long and 8–10 mm. wide when spread out, the base abruptly contracted into a short claw which apparently is articulated with the foot of the column, lateral lobes obliquely rhombic-triangular, obtuse, erect, the mid-lobe broadly spreading, somewhat concave, more or less transversely oblong-reniform, the apex sometimes shallowly emarginate; disk with a low, fleshy, tuberculate callus. Column short, stout, semi-terete, rather arcuate, 3–4 mm. long, the margins of the apex slightly projecting and forming a short hood over the clinandrium.

Panama, Colombia, Venezuela, British Guiana, and Brazil.

PANAMÁ: grassy ridges, vic. Cerro Jefe, hills east of Panama City, 2500 ft., *Rolland Jones s. n.* (under *Allen 3791*). COCLÉ: Loma del Tigre, hills north of El Valle de Antón, 3000 ft., *Allen 3562*.

61. ZYGOPETALUM Hook.

ZYGOPETALUM Hook. in Bot. Mag. *t. 2748.* 1827; Benth. & Hook. Gen. Pl. 3:542. 1883.

Zygopetalon Rchb. Consp. 69. 1828.
Galeottia A. Rich. in Ann. Sci. Nat. Bot. III, 3:25. 1845.

Epiphytic or terrestrial herbs. Pseudobulbs ovoid or subcylindric, tapering, the bases enveloped in several short or elongate, non-foliaceous or foliaceous bracts, the apex with 1 or 2 lanceolate or elliptic-lanceolate, plicate leaves. Inflorescences short or elongate, erect, racemose, produced from the base of the current growth; scape bracts small or large. Flowers few to many, small, or large and conspicuous. Sepals subequal, spreading, free or slightly connate at the base, the laterals adnate to the foot of the column, forming a short, broad mentum. Petals subequal to the sepals. Lip conspicuously or obscurely 3-lobed, the base affixed to, or articulated with, the column foot, the lateral lobes spreading or erect, the mid-lobe broadly spreading, or the apex strongly recurved; the disk with a prominent, fleshy, often lunate, tuberculate or cristate callus. Column rather short, stout, semi-terete, somewhat arcuate, the apex with or without conspicuous lateral wings, the base produced into a short foot. Anther terminal, operculate, incumbent, 2-celled; pollinia 4, waxy.

A polymorphic genus of American epiphytic and terrestrial herbs, ranging from southern Mexico to Peru and Brazil.

a. Plants epiphytic. Flowers large and conspicuous; lip 3-lobed, the margins fimbriate..... 1. Z. GRANDIFLORUM
aa. Plants terrestrial. Flowers small; lip subpandurate, the margins entire.... 2. Z. PARVIFLORUM

1. ZYGOPETALUM GRANDIFLORUM (A. Rich.) Benth. & Hook. ex Hemsl. Biol. Centr.-Amer. Bot. 3:251. 1883.

Galeottia grandiflora A. Rich. in Ann. Sci. Nat. Bot. III, 3:25. 1845.
Batemannia grandiflora Rchb. f. in Bonplandia 4:323. 1856.

Epiphytic herbs, with ovoid, somewhat furrowed pseudobulbs 3.5–6 cm. long and 2–3 cm. wide, enveloped at the base in 3–4 papery, imbricating bracts; the apex of the pseudobulbs with 2 elliptic-lanceolate, plicate, acute leaves 25–50 cm. long and 4–6.5 cm. wide. Inflorescences 15–18 cm. tall, produced from the base of the current flush of new growth. Flowers 1 to about 5, large and conspicuous, the pedicels subtended by broad, spathaceous, papery bracts. Sepals subequal, spreading, the apices recurved, green striped reddish brown, dorsal sepal free, lanceolate-acuminate, 3.0–4.5 cm. long and 1.0–1.5 cm. wide, laterals connate at the base and adnate to the foot of the column, forming a gibbose mentum, rather obliquely lanceolate, acuminate, 3.0–4.5 cm. long and 1.2–1.8 cm. wide. Petals subequal to the sepals, obliquely falcate, acuminate, spreading, the broad bases adnate to the sides of the column foot, the apices recurved, green striped reddish-brown, 3.0–4.0 cm. long and 1.2–1.8 cm. wide. Lip conspicuously 3-lobed, ab-

Fig. 175. *Zygopetalum grandiflorum*

ruptly contracted at the base, with a short claw which is articulated with the column foot, white with dull red or purple longitudinal markings, lateral lobes erect, rather obliquely acute, with fimbriate margins, mid-lobe obovate, acuminate, somewhat concave, the attenuate apex strongly recurved, the lateral margins fimbriate; disk between the lateral lobes with a broad, erect, lunate, prominently ridged and furrowed, multi-denticulate callus. Column broad, stout, arcuate, 1.5–2 cm. long, the apex with 2 short, denticulate processes on either side of which are 2 subfalcate, obliquely obtuse wings with ciliate apical margins; the base of the column produced into a short, broad foot.

Mexico, Guatemala, Costa Rica, and Panama.

CHIRIQUÍ: vic. Cerro Punta, headwaters of the Río Chiriquí Viejo, 2000 m., *Allen 3604.*

2. ZYGOPETALUM PARVIFLORUM L. Wms. apud Woodson & Schery, in Ann. Mo. Bot. Gard. 28:424, *t. 25.* 1941.

Erect, robust, terrestrial herbs, with slender, subcylindric, tapering pseudobulbs 6–9 cm. tall and about 1.5 cm. wide; leaves and blades of the foliaceous bracts linear-lanceolate to elliptic-lanceolate, plicate, acute or acuminate, the bracts contracted at the base into a short sheathing petiole, the imbricating bases completely enveloping the small pseudobulb. Leaves 30–70 cm. long and 2.5–7 cm. wide. Inflorescences 60–80 cm. tall, produced from the basal portion of the current flush of new growth. Flowers several or many, among the smallest in the genus, described as "purple, the lip violet; column white." Sepals subequal, rather fleshy, spreading, oblong-ovate, acute, 7–10 mm. long and 3.5–5 mm. wide. Petals subquadrate, obtuse, 7–8 mm. long and 4–4.5 mm. wide. Lip obscurely 3-lobed, subquadrate, panduriform, 7–8 mm. long and 5–6 mm. wide, abruptly contracted at the base, with a short claw which is articulated with the column foot, lateral margins rounded and spreading, mid-lobe rectangular, abruptly truncate, spreading; the disk with a broad, transverse, subreniform, fleshy callus. Column short, semi-terete, somewhat dilated at the apex, 4–5 mm. long. Anther and pollinia typical of the genus.

Panama.

CHIRIQUÍ: vic. Bajo Chorro, headwaters of the Río Caldera, 1900 m., *Woodson & Schery 605;* vic. Bajo Chorro, in rain forest, 6000 ft., *Davidson 345.*

62. CHONDRORHYNCHA Lindl.

CHONDRORHYNCHA Lindl. in Orch. Linden. 12. 1846; Rchb. f. in Walp. Ann. 6:663. 1863; Benth. & Hook. Gen. Pl. 3:548. 1883.

Kefersteinia Rchb. f. in Bot. Zeit. 10:633. 1852.
Warczewiczella Rchb. f. loc. cit. 635. 1852.
Warscewiczella Rchb. f. Xenia Orch. 1:61. 1858.
Warszewiczella Benth. & Hook. Gen. Pl. 3:543. 1883.

Tufted epiphytic herbs without pseudobulbs. Leaves distichously arranged in the form of an open fan, erect or arching, plicate, lanceolate, acute or acuminate, contracted below into conduplicate petioles. Inflorescences slender, erect, arching or semi-pendulous, 1-flowered, scapose, less than half the length of the leaves, produced from the axils of the lower leaves or bracts. Flowers small to large and conspicuous. Sepals subequal, free, spreading, membranaceous, the dorsal sepal erect, the laterals often retrorse, obliquely inserted on the short column foot. Petals usually spreading, subequal to the dorsal sepal or broader. Lip usually cucullate, obovate, suborbicular or subquadrate, sometimes obscurely or conspicuously 3-lobed, the lateral lobes or margins erect, or the lip explanate and divided into a narrow basal and a broad apical part, contracted at the base and adnate to, or articulated with, the very short column foot, sometimes forming a very short mentum; disk with a broad or narrow, more or less fleshy callus, the apex free and usually denticulate, or rarely with the basal callus conspicuously pedicellate, the apex scutellate. Column semi-terete, slender or broadly clavate above, sometimes narrowly winged, the ventral surface with or without a keel, rarely with a broad, 2-alate plate below the stigma, the base of the column produced into a very short foot. Anther terminal, operculate, incumbent, 1-celled or imperfectly 2-celled; pollinia 4, waxy.

a. Lip explanate, subpandurate, never concave or cucullate, divided into narrower basal and broader apical parts ..... 1. C. AROMATICA

aa. Lip concave or cucullate, entire or 3-lobed, suborbicular or obovate when spread out.

b. Lip entire when spread out. (See also alternate bb)

c. Flowers small; lip 1.2 cm. long or less.

d. Basal callus conspicuously pedicellate, the apex 2-scutellate ..... 3. C. COSTARICENSIS

dd. Basal callus sessile, the free apex bifid ..... 5. C. LACTEA

cc. Flowers relatively large and conspicuous; lip 2.5 cm. long or more.

d. Lateral margins of the basal callus erect, thickened, and confluent with the erect incurving lateral margins of the lip. Lowland species ..... 6. C. MARGINATA

dd. Lateral margins of the basal callus not erect, not thickened, nor confluent with the incurving lateral margins of the lip. Highland species.

e. Basal callus linear, the free apex bifid ..... 2. C. CALOGLOSSA

ee. Basal callus radiate, digitate, the free projecting apex with 5–7 elongate teeth of unequal length ..... 4. C. DISCOLOR

bb. Lip obscurely or conspicuously 3-lobed when spread out, 2.5 cm. long or more.

c. Lateral margins of the basal callus erect, thickened, and confluent with the erect incurving lateral margins of the lip. Lowland species ..... 6. C. MARGINATA

cc. Lateral margins of the basal callus not erect, not thickened, nor confluent with the erect incurving lateral margins of the lip. Highland species.

d. Basal callus linear, with a free bifid apex ..... 2. C. CALOGLOSSA

dd. Basal callus radiate, digitate, the free projecting apex with 5–7 elongate teeth of unequal length ..... 4. C. DISCOLOR

1. CHONDRORHYNCHA **aromatica** (Rchb. f.) P. H. Allen, comb. nov.

Zygopetalum aromaticum Rchb. f. in Bot. Zeit. 10:668. 1852.
Warscewiczella aromatica Rchb. f. in Walp. Ann. 6:654. 1863.
Zygopetalum Wendlandi Rchb. f. Beitr. Orch. Centr.-Amer. 74. 1866.
Bollea Wendlandiana Hort. ex Gard. & For. 1:315. 1888.
Warscewiczella Wendlandi (Rchb. f.) Schltr. in Beih. Bot. Centralbl. 36^2:494. 1918.

Erect tufted epiphytic herbs without pseudobulbs. Leaves linear-ligular to elliptic-lanceolate, plicate, acute or shortly acuminate, 15–30 cm. long and 1.5–2.5 cm. wide. Inflorescences erect or arching 1-flowered scapes 7–9 cm. long, from the axils of the non-foliaceous basal bracts. Flowers relatively large and conspicuous. Sepals subequal, free, spreading, pale green or yellowish green, the dorsal sepal elliptic-lanceolate, acuminate, 2.5–3 cm. long and .6–.8 cm. wide, the laterals lanceolate, acuminate, 2.8–3.2 cm. long and .9–1.0 cm. wide. Petals subequal to the dorsal sepal, spreading, pale or yellowish green, lanceolate, acuminate, 2.5–3 cm. long and .5–.6 cm. wide. Lip explanate, subpandurate, the base obscurely lobed, abruptly contracted into a short claw, lavender or violet, usually with white margins, 2.2–2.5 cm. long and 1.5–1.7 cm. wide, divided into a more or less rectangular basal half and a broader undulate and reflexed apex; disk with a lunate to radiate or rhombic, spreading, plurisulcate, violet-blue callus. Column short, erect, white, semi-terete below, the apex clavate and narrowly winged. Anther terminal, operculate, incumbent, 1-celled.

Costa Rica and Panama.

CHIRIQUÍ: without definite locality, 4000–5000 ft., *Powell 248*.

The flowers of our specimens seem to be somewhat smaller than typical Costa Rican material, but otherwise are identical.

2. CHONDRORHYNCHA **caloglossa** (Schltr.) P. H. Allen, comb. nov.

Warscewiczella caloglossa Schltr. in Fedde Rep. Sp. Nov. 12:216. 1913.
Chondrorhyncha estrellensis Ames, Sched. Orch. 4:54. 1923.

Erect tufted epiphytic herbs without pseudobulbs, 23–28 cm. tall, the plants typical of the genus. Inflorescences erect or arching, 1-flowered scapes 10–15 cm. long, from the axils of the lower foliaceous bracts. Flowers relatively large and conspicuous. Sepals subequal, membranaceous, free, white or pale yellow, the dorsal sepal erect, lanceolate, acute or acuminate, 2.8–3.2 cm. long and .6–.7 cm. wide, laterals obliquely inserted, deflexed, concave, lanceolate, acute or acuminate, 3–3.5 cm. long and .6–.7 cm. wide. Petals spreading, white or pale yellow, elliptic-oblanceolate, acute, 3–3.5 cm. long and 1.2–1.4 cm. wide. Lip concave, entire or obscurely or conspicuously 3-lobed when spread out, white or pale yellow, reticulated purple, 2.8–3.5 cm. long and 2–2.5 cm. wide; disk smooth, with a linear-ligular yellow callus, the free projecting apex bifid. Column semi-terete, 1.2–1.4 cm. long. Anther and pollinia typical of the genus.

Costa Rica and Panama.

CHIRIQUÍ: humid forest around Los Siguas Camp, southern slope of Cerro Horqueta, 1700 m., *Pittier 3176;* Cuesta de las Palmas, Cerro Horqueta, 1700–2100 m., *Pittier 3214, Maxon 5510;* vic. Bajo Chorro, rain forest, 6000 ft., *Davidson 93;* trail from Cerro Punta to the headwaters of the Río Caldera, 2250–2500 m., *Allen 1462.*

A somewhat variable species, the flowers reminiscent of those of *Chondrorhyncha discolor,* but readily separable by the reticulated color pattern and narrow, bifid callus of the lip.

3. CHONDRORHYNCHA **costaricensis** (Schltr.) P. H. Allen, comb nov.

Kefersteinia costaricensis Schltr. in Beih. Bot. Centralbl. 36^2:413. 1918.

Dwarf tufted epiphytic herbs without pseudobulbs, 12–18 cm. tall. Leaves plicate, lanceolate, acuminate, 10–18 cm. long and 1.5–2 cm. wide. Inflorescences of slender, arching or semi-pendulous scapes 2.5–4 cm. long, from the base of the leaves. Flowers small, solitary. Sepals subequal, spreading, white or cream, the dorsal sepal elliptic-lanceolate, acute or subacute, 8–10 mm. long and 4–5 mm. wide, lateral sepals rather obliquely elliptic-lanceolate, acute or apiculate, 10–12 mm. long and 5–6 mm. wide. Petals subequal to the dorsal sepal, white or cream, often spotted maroon, obliquely oblong, acute, 7–9 mm. long and 4–5 mm. wide. Lip entire, suborbicular, contracted at the base and adnate to the foot of the column, 8–10 mm. long and 7–8 mm. wide, white or cream, spotted maroon, the apex entire or with an obtuse apicule; disk with an erect pedicellate callus, the apex 2-scutellate. Column erect, 5–7 mm. long, the apex broadly clavate, the ventral surface with a longitudinal keel which is expanded into a broad biauriculate, abruptly apiculate plate below the narrow transverse stigma. Anther terminal, operculate, incumbent, 1-celled.

Costa Rica and Panama.

COLÓN: Río Llano Sucio, vic. Puerto Pilón, about 65 m., *H. P. Butcher s. n.* (under *Allen 2457*).

Known in Panama from a single fragmentary specimen preserved in liquid. Our material shows some slight differences from the Costa Rican type, notably in the subrhombic rather than scutellate divisions of the apex of the basal callus, and the apparently fleshier winged plate below the stigma, which has a more prominent central spur or apicule. Although it has been decided to consider our specimen as representing *Chondrorhyncha costaricensis,* it would seem well to note that this, and apparently one or two other species from outside our range, exhibit a radical departure from the typical concept of either *Chondrorhyncha* or *Kefersteinia* in the conspicuously pedicellate basal callus of the lip and the broad plate on the under-side of the column below the stigma. It seems possible that these may actually represent an unrecognized entity of generic rank. Unfortunately, these characters are not always easily seen in dried specimens. However, the necessity for adequate material to show points of difference in no way alters the basic fact that they may exist.

Due to our present very limited and somewhat fragmentary material, it is thought best to follow established usage for the purposes of this treatment.

4. CHONDRORHYNCHA **discolor** (Lindl.) P. H. Allen, comb. nov.

Warrea discolor Lindl. in Jour. Hort. Soc. Lond. 4:265. 1849.
Warscewiczella discolor (Lindl.) Rchb. f. in Bot. Zeit. 10:636. 1852.
Zygopetalum discolor (Lindl.) Rchb. f. in Walp. Ann. 6:655. 1861.

Erect, tufted, epiphytic or pseudo-terrestrial herbs without pseudobulbs, 20–35 cm. tall, the plants typical of the genus. Inflorescences of slender, erect or arching, 1-flowered scapes 7–15 cm. long, produced from the axils of the lower non-foliaceous bracts. Flowers relatively large and conspicuous, sometimes nodding. Sepals membranaceous, subequal, free, spreading, white, often with yellowish apices, dorsal sepal erect, elliptic-lanceolate, acute, the apex recurved, 2.8–3 cm. long and 1.0–1.5 cm. wide, laterals deflexed, concave, lanceolate, acute, 3–3.2 cm. long and .8–1.0 cm. wide. Petals spreading, elliptic, obtuse to subacute, white, often suffused with purple toward the apex, 2.5–3 cm. long and 1.2–1.5 cm. wide. Lip cucullate, obscurely to conspicuously 3-lobed when spread out, 2.5–3.2 cm. long and 2.2–3 cm. wide, deep violet-purple, sometimes with narrow whitish margins, lateral lobes or margins erect and incurving over the column, the apex suborbicular and slightly retuse; disk with a radiate, digitate, plurisulcate callus, the free projecting apex with elongate teeth of unequal length. Column short, semiterete, narrowly clavate, 10–12 mm. long, white, sometimes blotched with purple. Anther and pollinia typical of the genus.

Cuba, Costa Rica, and Panama.

CHIRIQUÍ: without definite locality, 4500–5500 ft., *Powell 155;* upper Río Chiriquí Viejo, vic. Monte Lirio, *G. White 42;* llanos and slopes of Chiriquí Volcano and along the Río Chiriquí Viejo, 1200 m., *Allen 914.*

A very frequent species of the Chiriquí highlands, where the plants are often found in association with those of *Odontoglossum Schlieperianum*, as epiphytes on low trees or sometimes as pseudo-terrestrials on boulders and steep mossy banks.

5. CHONDRORHYNCHA LACTEA (Rchb. f.) L. Wms. in Caldasia 5:16. 1942.

Zygopetalum lacteum Rchb. f. in Gard. Chron. 1290. 1872.
Kefersteinia lactea Rchb. f. apud B. D. Jackson in Index Kew. 2:4. 1895.

Epiphytic herbs without pseudobulbs, the plants usually consisting of tufted clusters of several distichous crowns of relatively broad plicate leaves, which are oblong to elliptic-lanceolate, acute, 6–12 cm. long and 1.2–2 cm. wide, the basal portions somewhat contracted into a stout petiole. Inflorescences very short, filiform, more or less arching, or erect scapes about 1.5 cm. long, produced from the lower leaf axils. Flowers small, solitary. Sepals subequal, free, spreading, elliptic-lanceolate, obtuse to subacute, 8–10 mm. long and 3–4 mm. wide. Petals subequal to the sepals, elliptic-lanceolate, acute, 7–9 mm. long and 3–4 mm. wide. Lip undivided, suborbicular, 6–10 mm. long and 6–10 mm. wide when spread out,

abruptly contracted at the base into a short claw which is apparently articulated with the base of the column, the apex entire, shallowly emarginate or with an obtuse apicule; disk with a low, fleshy, sessile, bifid callus. Column semi-terete, 5–6 mm. long, the ventral surface below the stigma with a longitudinal keel. Anther and pollinia typical of the genus.

Costa Rica and Panama.

CHIRIQUÍ: without definite locality, *Wallis s. n.*

The species was described by Reichenbach from plants presumably collected in Chiriquí Province, the actual locality being unknown. Since there have been several subsequent collections from the Pacific slope in adjacent Costa Rica, there is every reason to believe that this rather obscure record may be good.

6. CHONDRORHYNCHA **marginata** (Rchb. f.) P. H. Allen, comb. nov.

Warczewiczella marginata Rchb. f. in Bot. Zeit. 10:636. 1852.
Huntleya marginata Hort. ex Rchb. f. loc. cit. 1852.
Warrea marginata Rchb. f. loc. cit. 1852.
Warrea quadrata Lindl. in Gard. Chron. 647. 1853.
Warscewiczella velata Rchb. f. in Bot. Zeit. 23:99. 1865.
Zygopetalum quadratum Pfitz. Vergl. Morph. Orch. 58. 1881.
Chondrorhyncha Lipscombiae Rolfe, in Kew Bull. 133. 1912.

Tufted epiphytic herbs without pseudobulbs. Leaves 5–7, linear, elliptic-oblanceolate, acute, 12–30 cm. long and 2–4.5 cm. wide, firm, arching, contracted below into conduplicate petioles the lowest pair being little more than foliaceous bracts. Inflorescences of slender, arching or semi-pendulous, 1-flowered scapes, 5.5–10 cm. long, from the axils of the lowest non-foliaceous bracts. Flowers the largest of the genus in Panama, with a very agreeable and characteristic fragrance during the morning hours, reminiscent of cinnamon or cloves. Sepals subequal, free, membranaceous, elliptic-lanceolate, acute, white, the dorsal sepal erect, somewhat concave, the apex recurved, 2.2–3 cm. long and .9–1.2 cm. wide, the laterals usually more or less conduplicate, obliquely reflexed, 2.8–3.2 cm. long and .8–1.0 cm. wide. Petals membranaceous, spreading, white, usually with a lavender median line, elliptic-lanceolate, acute, 2.5–3 cm. long and 1.0–1.2 cm. wide, the apices recurved. Lip white, with a conspicuous pattern of radiating, often divaricate, lavender or pinkish lavender lines, cucullate, subquadrate to obscurely 3-lobed when spread out, 3.5–4.5 cm. long and 3–3.5 cm. wide, contracted at the base and adnate to the short column foot, the lateral lobes or margins erect and incurved over the column, the frontal margin broadly spreading, often suffused with lavender or pinkish lavender, entire, or emarginate at the apex; the disk between the erect lateral lobes or margins with a broadly spreading, fleshy, plurisulcate callus, white striped lavender, the lateral margins of which are thickened and confluent with the erect lateral lobes of the lip and the apex more or less broadly truncate, free, the many short projecting teeth all of about equal length. Column semi-terete below, dilated and broadly clavate above, pure white, 12–18 mm. long. Anther terminal, operculate, incumbent, 1-celled.

Fig. 176. *Chondrorhyncha marginata*

Panama and Colombia.

CANAL ZONE: Cacao Plantation, near Summit, *Lipscomb s. n.;* Summit, *Powell 3483;* Barro Colorado Island, *J. Zetek s. n.;* vic. Frijoles, *Powell 3460;* Gatún Lake region, *Powell 11, 47;* Cacao Plantation, vic. Summit, *Florence & James Barrett s. n.* PANAMÁ: western arm of the Quebrada Salamanca, 70 m., *Dodge, Steyermark & Allen 16989.* COCLÉ: damp shaded valleys south of El Valle de Antón, 600 m., *Allen 2843.*

A fairly frequent and attractive species, found in damp shaded locations usually at low elevations.

63. PESCATOREA Rchb. f.

PESCATOREA Rchb. f. in Bot. Zeit. 10:667. 1852; Benth. & Hook. Gen. Pl. 3:543. 1883.

Erect, tufted, epiphytic herbs without pseudobulbs. Leaves plicate, contracted below into conduplicate imbricating petioles, which are distichously arranged in the form of an open fan. Inflorescences of short, slender, arching, 1-flowered scapes produced from the axils of the non-foliaceous basal bracts. Flowers relatively large and conspicuous. Sepals more or less fleshy, subequal, concave, the dorsal sepal erect, free, the laterals connate at the base and obliquely inserted on the column foot. Petals subequal to the sepals. Lip rather fleshy, 3-lobed, abruptly contracted at the base into a conspicuous ligular claw which is continuous with the foot of the column, the limb forming an obtuse angle with the column foot, the base apparently with a deep concavity below the column, surrounded by an erect semicircular plurisulcate callus; apical lobe of the lip more or less convex or ventricose, the lateral margins often recurved. Column stout, semi-terete, produced at the base into a short foot. Anther terminal, operculate, incumbent, 1-celled; pollinia 4, waxy.

A small genus of tufted pseudobulbless epiphytes, ranging from Costa Rica to Colombia. The genus is sometimes considered as being referable to *Warscewiczella,* and has been so treated in the main generic key.

In the exceedingly perplexing association of closely allied generic concepts embracing *Bollea, Chondrorhyncha, Kefersteinia, Huntleya, Pescatorea, Warscewiczella,* and *Zygopetalum,* it becomes largely a matter of individual opinion which are to be rejected and which retained. Probably something very nearly approaching a logical treatment of the situation was proposed by Reichenbach *filius* (in Walp. Ann. 6:650–662. 1863) in his reduction of nearly all of these to sections of *Zygopetalum.* This solution has never been universally accepted, however, the more recent tendency being to recognize some as valid genera and to reduce others to synonymy. Here, as in most other cases of a similar nature, no hard-and-fast rule can be applied. Most genera, when examined critically, are found to be more or less arbitrary segregations, and should be recognized as being conveniences and a means to an end.

Dr. Louis O. Williams has suggested that *Kefersteinia* is referable to *Chondrorhyncha,* a view in which I, for the most part, concur since the generic type,

K. graminea (Lindl.) Rchb. f., and most of the subsequently described species are structurally nearly identical with *Chondrorhyncha;* yet there are other Kefersteinias, notably *K. costaricensis* Schltr., which differ radically from this generic concept. The type species of *Warszewiczella, W. discolor* (Lindl.) Rchb. f., also is almost identical with the earlier *Chondrorhyncha,* and apparently should be reduced; but not including *Pescatorea,* which seems to have ample characters upon which to base segregation. For the purposes of this treatment, the following alternate key is proposed for the separation of the genera in our area:

KEY TO THE GENERA

a. Plants with pseudobulbs. Inflorescences racemose, several- to many-flowered..... 61. ZYGOPETALUM

aa. Plants without pseudobulbs. Inflorescences of short 1-flowered scapes.

b. Lip truly clawed at the base, explanate or convex, never cucullate.

c. Apex of the column semiterete, never with broad projecting lateral wings. Basal callus plurisulcate, never fimbriate..... 63. PESCATOREA

cc. Apex of the column with broad projecting lateral wings, forming a conspicuous hood over the clinandrium. Basal callus fimbriate.... 64. HUNTLEYA

bb. Lip obscurely clawed at the base, usually convex or cucullate, rarely explanate..... 62. CHONDRORHYNCHA

1. PESCATOREA CERINA (Lindl.) Rchb. f. in Bot. Zeit. 10:667. 1852.

Huntleya cerina Lindl. & Paxt. in Paxton's Flow. Gard. 3:62. 1852–53.
Zygopetalum cerinum (Lindl.) Rchb. f. in Walp. Ann. 6:651. 1863.

Tufted epiphytic herbs without pseudobulbs. Leaves erect or arching, plicate, subcoriaceous, linear-lanceolate to elliptic-lanceolate, acute or acuminate, 15–60 cm. long and 3–5 cm. wide. Inflorescences of short, 1-flowered, erect or arching scapes 3.5–10 cm. long, from the axils of the basal non-foliaceous bracts. Flowers large and conspicuous. Sepals subequal, rather fleshy, concave, spreading, the dorsal sepal free, white, linear-elliptic to obovate, obtuse, 2.5–3.2 cm. long and 1.6–1.8 cm. wide, laterals somewhat connate at the base, obliquely inserted on the column foot, white with a long greenish-yellow blotch near the base, elliptic-lanceolate to oblanceolate, obtuse, 2.5–3.5 cm. long and 1.8–2 cm. wide. Petals spreading, subequal to the dorsal sepal, white, inserted on the base of the column, spatulate to oblanceolate, obtuse, 2.5–3 cm. long and 1.5–1.8 cm. wide. Lip rather fleshy, 3-lobed, 2–3 cm. long and about 2.5 cm. wide, rich yellow, the basal callus marked reddish brown, abruptly contracted at the base into a conspicuous ligular claw which is continuous with the column foot, the limb forming an obtuse geniculate angle with the claw, the subfalcate lateral lobes resting against the base of the column, forming a deep concavity which is surrounded by a conspicuous erect, semicircular, plurisulcate callus, the frontal lobe convex to slightly ventricose, the apical margins often reflexed. Column short, stout, white, semiterete, 1.3–1.5 cm. long, produced at the base into a short foot. Anther terminal, lavender.

Costa Rica and Panama.

PANAMÁ: Cerro Campana, in cloud forest near summit, 2500–3000 ft., *Allen 4447,*

Fig. 177. *Pescatorea cerina*

5169. COCLÉ: vic. La Mesa, region north of El Valle de Antón, 1000 m., *Allen 2362.* VERAGUAS: forested slopes of Cerro Tuté, region west of Santa Fé, 2500–3000 ft., *Allen 4564, 5171.* CHIRIQUÍ: without definite locality, 4500 ft., *Purdom s. n.*

An attractive species of the wet highland forests of the Pacific slope, usually being found in shaded situations at about 3000 ft. elevation.

64. HUNTLEYA Batem. ex Lindl.

HUNTLEYA Batem. ex Lindl. in Bot. Reg. 23: post *t. 1991*. 1837; Benth. & Hook. Gen. Pl. 3:543. 1883.

Erect, tufted, epiphytic herbs without pseudobulbs. Leaves plicate, subcoriaceous, linear-lanceolate, acute, the bases somewhat conduplicate and imbricating, distichously arranged in the form of a fan. Inflorescences of slender, elongate, erect, 1-flowered scapes produced from the axils of the central leaves. Flowers large and conspicuous. Sepals rather fleshy, subequal, spreading, the dorsal sepal free, the laterals connate at the base and obliquely inserted on the column foot. Petals rather fleshy, spreading, subequal to the sepals, inserted on the foot of the column. Lip fleshy, abruptly contracted at the base, with a conspicuous claw which forms a geniculate angle with the column foot; the basal callus with an erect, semicircular, fimbriate margin, the apical lobe articulated with the base of the callus plate. Column short, somewhat arcuate, the apex dilated, with a dorsal keel, the lateral margins broadly winged and confluent at the apex, forming a conspicuous hood over the clinandrium. Anther terminal, operculate, incumbent, 1-celled or imperfectly 2-celled; pollinia 4, waxy.

About three or four species of American epiphytes, ranging from Costa Rica to Brazil. They often are listed as Zygopetalums. One species is known from Panama.

1. HUNTLEYA MELEAGRIS Lindl. in Bot. Reg. 23: post *t. 1991*. 1837.

Batemannia Burtii Endres & Rchb. f. in Gard. Chron. 1099. 1872.
Zygopetalum meleagris Benth. in Jour. Linn. Soc. 18:321. 1880.
Zygopetalum Burtii Benth. & Hook. ex Hemsl. Biol. Centr.-Amer. Bot. 3:251. 1883.
Huntleya Burtii (Endres & Rchb. f.) Rolfe, in Orch. Rev. 24:236. 1916.

Erect, tufted, epiphytic herbs without pseudobulbs. Leaves plicate, subcoriaceous, linear-lanceolate to elliptic-lanceolate, acute, 15–30 cm. long and 3–4.5 cm. wide. Inflorescences of erect 1-flowered scapes 10–15 cm. tall produced from the axils of the central leaves. Flowers large and conspicuous. Sepals subequal, fleshy, spreading, elliptic-lanceolate, acute to acuminate, the margins undulate, the apical ⅔ a waxy reddish brown, usually with some yellow spots, the basal ⅓ white or pale yellow, the dorsal sepal free, 4–6 cm. long and 2–2.5 cm. wide, the laterals connate at the base and obliquely inserted on the column foot, 4.5–6 cm. long and 1.5–2.5 cm. wide. Petals fleshy, spreading, subequal and colored similarly to the sepals, with purple blotches or streaks at the base near the insertion on the column foot, broadly elliptic-lanceolate, acuminate, with undulate margins, 3.5–5.6 cm. long and 2–3 cm. wide. Lip fleshy, the base nearly white or yellowish, the frontal half of the apical lobe usually a rich waxy reddish brown or brownish purple, 2.5–3.5 cm. long and 2–3 cm. wide, the base of the lip abruptly contracted, with a conspicuous claw which forms a geniculate angle with the foot of the column, the basal callus with an erect semicircular fimbriate crest, the posterior margins of which are incumbent on the foot of the column, the apical lobe obscurely 3-

Fig. 178. *Huntleya meleagris*

lobulate, obovate, acute to acuminate, contracted at the base and articulated with the apex of the callus plate, the lateral lobules rounded, spreading, the apical lobule broadly triangular, the acuminate apex recurved. Column stout, erect, 1.5–2 cm. long, semiterete below, dilated above, with a conspicuous dorsal keel and broad lateral wings which are confluent at the apex, forming a hood over the clinandrium. Anther terminal, operculate, incumbent, imperfectly 2-celled.

Costa Rica, Panama, Colombia, and Brazil.

COCLÉ: western slope and summit of Cerro Valle Chiquito, 700–800 m., *Seibert 643;* trail to Las Minas, region north of El Valle de Antón, 1000 m., *Allen 2894.*

A rare species of the wet highland forests, growing in deep shade at elevations above 2500 ft. The plants are often associated with a *Brassia* of nearly identical vegetative appearance, and are exceedingly difficult to distinguish when not in flower. The conduplicate bases of the leaves of the *Brassia* are often slightly broader below the suture line, while those of the *Huntleya* are of uniform width. The Central American plants have hitherto been called *Huntleya Burtii,* but other than some slight difference in size and color our material seems identical with specimens collected in Brazil.

65. MAXILLARIA Ruiz & Pavon

MAXILLARIA Ruiz & Pavon, Fl. Peruv. & Chil. Prodr. 116, *t. 25.* 1794; Lindl. in Bot. Reg. n. s. 6: Misc. 10. 1843; Benth. & Hook. Gen. Pl. 3:555. 1883.

Ornithidium Salisb. in Trans. Hort. Soc. Lond. 1:293. 1812.
Camaridium Lindl. in Bot. Reg. 10: *t. 844.* 1824.
Psittacoglossum La Llave & Lex. Nov. Veg. Desc. 2:29. 1825.
Heterotaxis Lindl. in Bot. Reg. 12: *t. 1028.* 1826.
Dicrypta Lindl. Gen. & Spec. Orch. Pl. 44. 1830.
Menadena Raf. Fl. Tellur. 2:98. 1836.
Onkeripus Raf. loc. cit. 4:42. 1836.
Pentulops Raf. loc. cit. 4:42. 1836.

Epiphytic herbs with very short to elongate, often branching, erect, arching or pendulous stems, with or without clustered or distant, 1- to 3-leaved pseudobulbs. Leaves persistent, conduplicate in vernation, usually coriaceous or fleshy, rarely thin, usually strap-shaped, without prominent veins. Inflorescences of 1 to many, reduced to elongate, 1-flowered scapes from the bases of the pseudobulbs, from the axils of the leaves, or the flush of new growth. Flowers small to large and conspicuous. Sepals subequal, free, or the laterals somewhat connate at the base, adnate to the foot or base of the column, often forming a short mentum. Petals subequal to the sepals or somewhat smaller. Lip concave, 3-lobed or entire, sessile or contracted at the base into a short claw, articulated with or adnate to the foot or base of the column, lateral lobes or margins erect, the mid-lobe membranaceous or thickened, spreading or reflexed; disk rarely without a fleshy callus. Column erect, semi-terete, somewhat arcuate, not winged, the base with a short foot, or footless. Anther terminal, operculate, incumbent, 1-celled or imperfectly 2-celled; pollinia 4, waxy.

About 250 species of tropical American epiphytes, ranging from Mexico to Peru, Brazil, and the West Indies. As would be expected from a large group of plants having a great geographic range, they vary considerably in size and vegetative habit. The species can roughly be separated into two main divisions. In the first division the pseudobulbs are conspicuously present, either as sessile clusters or distributed along the rhizome; while in the second division the pseudobulbs are inconspicuous or entirely absent, the plants usually either erect canes with 2-ranked foliage, or with sessile clusters of leaves in the form of a fan. However, there are many species in which conspicuous pseudobulbs are at first produced at the base, the subsequent growth becoming elongate, often branching or scandent, lacking pseudobulbs, or with pseudobulbs small and hidden by the imbricating leaf bases. Plants of some of these modified types are often indistinguishable from those of *Camaridium* and *Ornithidium*, the first of which in particular is a highly technical and arbitrary generic concept. In accordance with recently accepted usage, both of these are here considered to be Maxillarias. At the present time, some 41 species are known from Panama.

a. Secondary stems usually conspicuously thickened into pseudobulbs. (See also section aa.)
  b. Plants caespitose. Rhizome very short; pseudobulbs erect, usually congested (rarely solitary), apex monophyllous.
    c. Bracts enveloping the base of the pseudobulb conspicuously foliaceous.
      d. Bases of the foliaceous bracts completely covering the poorly developed pseudobulb ..... 14. M. CRASSIFOLIA
      dd. Bases of the foliaceous bracts covering only the basal half of the well-developed pseudobulb.
        e. Plants small. Foliaceous bracts 1–2. Sepals 5 mm. wide or less. Mentum elongate ..... 13. M. CONFUSA
        ee. Plants large. Foliaceous bracts 3 or more. Sepals 8 mm. wide or more. Mentum short ..... 25. M. MALEOLENS
    cc. Bracts enveloping the bases of the pseudobulbs not or apparently not foliaceous.
      d. Mid-lobe of the lip ½ or more of the total length of the lip.
        e. Apices of the lateral lobes of the lip acute, conspicuously projecting ..... 35. M. RUFESCENS
        ee. Apices of the lateral lobes of the lip not acute, not conspicuously projecting ..... 16. M. CUCULLATA
      dd. Mid-lobe of the lip less than ½ the total length of the lip.
        e. Pseudobulbs complanate-cylindric, apparently continuous with the leaf petiole ..... 5. M. ARACHNITIFLORA
        ee. Pseudobulbs ovoid to elliptic-ovoid, compressed, but never cylindric, broader than the leaf petioles.
          f. Plants small, up to 25 cm. tall.
            g. Mid-lobe about ½ the total length of the lip. Apex of the pseudobulb subacute ..... 23. M. LONGIPETIOLATA
            gg. Mid-lobe about ⅓ the total length of the lip. Apex of the pseudobulb broadly truncate.
              h. Mentum short, acute. Sepals acute, 15 mm. or less long ..... 9. M. BREVIPES
              hh. Mentum elongate, acuminate. Sepals acuminate, 17 mm. or more long ..... 13. M. CONFUSA
          ff. Plants large, more than 25 cm. tall (usually much taller).
            g. Flowers relatively large. Sepals 4 cm. or more long.
              h. Sepals obtuse to subacute, about 10 mm. wide ..... 24. M. LUTEO-ALBA
              hh. Sepals acuminate, about 6 mm. wide ..... 3. M. ANGUSTISEGMENTA
            gg. Flowers relatively small. Sepals 3.5 cm. or less long.

h. Mid-lobe about ½ the total length of the lip. Apex of the pseudobulb subacute..... 23. M. LONGIPETIOLATA
hh. Mid-lobe about ⅓ the total length of the lip. Apex of the pseudobulb broadly truncate.
i. Sepals 2.5 cm. long or more..... 34. M. RINGENS
ii. Sepals 2 cm. long or less..... 32. M. POWELLII
bb. Plants caulescent. Rhizomes or canes elongate, sometimes branching; pseudobulbs approximate or distant, usually inserted on the rhizome at an oblique angle, sometimes confined to the base of the plant, erect, solitary or clustered.
c. Pseudobulbs distributed along the rhizome, approximate, the internodes not equaling the length of the pseudobulbs, often more or less imbricating (i. e., with the base of each pseudobulb covered by the apical portion of that preceeding it).
d. Flowers produced from the base of the current mature pseudobulb.
e. Bracts enveloping the bases of the pseudobulbs foliaceous.
f. Apical lobe of the lip about ⅔ of the total length..... 38. M. VAGANS
ff. Apical lobe of the lip about ⅓ of the total length..... 28. M. OREOCHARIS
ee. Bracts enveloping the bases of the pseudobulbs not or apparently not foliaceous.
f. Pseudobulbs minute, usually completely hidden by the papery imbricating bracts. Leaves very fleshy, subulate-conduplicate, rarely lanceolate-elliptic. Lip concave, entire, linear-spatulate..... 37. M. UNCATA
ff. Pseudobulbs conspicuous, not hidden by the bases of the imbricating bracts. Leaves coriaceous, ligular, or subulate-conduplicate. Lip entire or 3-lobed.
g. Scapes very short, in dense subsessile fascicles. Flowers enclosed in 2 conspicuous glumaceous bracts. Sepals broadly ovate, about 6 mm. long. Lip 3-lobed. Column footless..... 27. M. NEGLECTA
gg. Scapes conspicuously pedicellate, solitary or in loose fascicles. Sepals acute or obtuse. Lip entire, or obscurely 3-lobed. Column produced into a distinct foot.
h. Apex of the pseudobulbs 2- to 3-leaved. Scapes usually loosely fasciculate. Sepals acuminate..... 20. M. FRIEDRICHSTHALII
hh. Apex of the pseudobulbs monophyllous. Scapes usually solitary.
i. Leaves 25 cm. or more long. Pseudobulbs strongly ancipitous. Sepals acute to acuminate..... 28. M. OREOCHARIS
ii. Leaves 15 cm. long or less. Pseudobulbs usually not strongly ancipitous. Sepals broadly obtuse..... 40. M. VARIABILIS
dd. Flowers produced from the bract axils of the flush of new growth.
e. Leaves 25 cm. or more long.
f. Bracts of the flush of new growth acuminate. Mid-lobe of the lip conspicuously thickened..... 1. M. ALBA
ff. Bracts of the flush of new growth broadly obtuse. Mid-lobe of the lip not conspicuously thickened..... 10. M. CAMARIDII
ee. Leaves 18 cm. long or less.
f. Lip conspicuously 3-lobed, the mid-lobe more than ½ the total length of the lip..... 38. M. VAGANS
ff. Lip obscurely 3-lobed, the mid-lobe about ⅓ the total length of the lip..... 40. M. VARIABILIS
cc. Pseudobulbs distant to very distant on the rhizome, or confined to the base of the plant.
d. Pseudobulbs distant to very distant on the rhizome.
e. Flowering scapes produced from the axils of the current flush of new growth.
f. Pseudobulbs diphyllous.

g. Leaf petioles very short, the apices of the leaves obtuse. Bracts of the flush of new growth broadly obtuse..... 10. M. CAMARIDII
gg. Leaf petioles elongate, the apices of the leaves acute. Bracts of the flush of new growth acuminate..... 15. M. CTENOSTACHYA
ff. Pseudobulbs monophyllous.
g. Flowers minute, the sepals less than 8 mm. long.
h. Pseudobulbs suborbicular..... 26. M. MINOR
hh. Pseudobulbs linear..... 41. M. WERCKLEI
gg. Flowers of moderate size, the sepals more than 8 mm. long.
h. Pseudobulbs linear. Leaves less than 3 cm. long..... 41. M. WERCKLEI
hh. Pseudobulbs elliptic-ovate to elliptic-oblong. Leaves more than 6 cm. long.
i. Lip conspicuously 3-lobed when spread out.
j. Mid-lobe about ⅓ the total length of the lip..... 1. M. ALBA
jj. Mid-lobe more than ½ the total length of the lip.
k. Lateral lobes of the lip subfalcate, the mid-lobe acute to acuminate. Sepals acuminate..... 36. M. UMBRATILIS
kk. Lateral lobes of the lip rounded or broadly acute, the mid-lobe obtuse or subacute. Sepals acute..... 38. M. VAGANS
ii. Lip entire or obscurely 3-lobed, subpandurate when spread out..... 18. M. DIUTURNA
ee. Flowering scapes produced from the base of the current mature pseudobulb.
f. Flowers small, produced in dense subsessile fascicles. Column without a foot..... 27. M. NEGLECTA
ff. Flowers of moderate size, usually 1–3, each flower solitary in the bract axil, never produced in dense subsessile fascicles. Column with a distinct foot.
g. Leaves linear, elongate, less than 1 cm. wide. Sepals about 1.5 cm. long..... 28. M. OREOCHARIS
gg. Leaves broadly ligular, more than 3 cm. wide. Sepals about 3.5 cm. long..... 31. M. PLANICOLA
dd. Pseudobulbs confined to the base of the plant.
e. Flowers large and conspicuous. Sepals 3.5 cm. long or more.
f. Lip obscurely 3-lobed, about 1.5 cm. long..... 22. M. INAUDITA
ff. Lip conspicuously 3-lobed, about 1 cm. long..... 8. M. BRADEORUM
ee. Flowers small. Sepals 1.5 cm. long or less.
f. Sepals broadly ovate. Lip geniculate, sigmoid when seen in profile..... 21. M. FULGENS
ff. Sepals acute to acuminate, not broadly ovate. Lip not geniculate nor sigmoid in profile.
g. Lip distinctly 3-lobed, lateral lobes auriculate, erect..... 6. M. BIOLLEYI
gg. Lip entire..... 30. M. PITTIERI
aa. Secondary stems not, or rarely, or obscurely thickened into pseudobulbs, or the pseudobulbs confined to the base of the plant.
b. Plants caespitose.
c. Leaf bases conduplicate, imbricating, distichously arranged in the form of a broad fan.
d. Leaves fleshy. Flowers with short pedicels, subsessile in the central leaf axils.
e. Leaves many, equitant, gladiate, acuminate. Plants pendent.... 39. M. VALENZUELANA
ee. Leaves few, ligular, acute or obtuse, the conduplicate bases completely enveloping a small pseudobulb. Plants erect.
f. Plants more than 15 cm. tall. Leaves more than 15 mm. wide..... 14. M. CRASSIFOLIA
ff. Plants less than 10 cm. tall. Leaves less than 10 mm. wide.. 7. M. BRACHYBULBON
dd. Leaves subcoriaceous. Flowers with long pedicels, produced from the axils of the basal conduplicate bracts..... 11. M. CHARTACIFOLIA
cc. Leaf bases contracted below into narrow sheathing petioles, or apparently so.

d. Leaves fleshy, obtuse, with short, conduplicate, imbricating petioles. Inflorescences subsessile in the leaf axils..... 14. M. CRASSIFOLIA
dd. Leaves coriaceous, acute or acuminate. Flowers usually long-pedicellate, rarely subsessile in the leaf axils.
e. Leaves broad, 2.5 cm. wide or more. Flowers large, the sepals 4 cm. long or more..... 5. M. ARACHNITIFLORA
ee. Leaves narrow, .8 cm. wide or less. Flowers small, the sepals 2.5 cm. long or less.
f. Plants dwarf, usually less than 6 cm. tall..... 7. M. BRACHYBULBON
ff. Plants elongate, leaves 45 cm. or more long..... 4. M. ANGUSTISSIMA
bb. Plants caulescent, the elongate canes or rhizomes repent, erect or pendulous, sometimes with pseudobulbs at the base. Leaves 2-ranked on the stem.
c. Canes or rhizomes undivided, or apparently so.
d. Plants dwarf, 15 cm. tall or less.
e. Leaves acute or acuminate..... 37. M. UNCATA
ee. Leaves obtuse, or the apices retuse..... 41. M. WERCKLEI
dd. Plants more than 25 cm. tall.
e. Leaves forming a distichous, fasciculate cluster at the apex of the stems, the imbricating bases sometimes enveloping a small pseudobulb..... 21. M. FULGENS
ee. Leaves equidistantly distributed along the upper stems, the bases not fasciculate.
f. Leaves 9 cm. long or less, the apex retuse. Flowers small, the sepals 1.5 cm. long or less.
g. Sepals about 1.5 cm. long. Lip conspicuously 3-lobed, the basal lobes auriculate, erect, the apical lobe large, broadly obtuse..... 6. M. BIOLLEYI
gg. Sepals about 1 cm. long. Lip linear, concave, rather obscurely 3-lobed, the apical lobe small, acute..... 2. M. ALLENII
ff. Leaves 15 cm. or more long, the apex broadly obtuse to acuminate. Flowers relatively large, the sepals 2.5 cm. long or more.
g. Lip about 9 mm. long, conspicuously 3-lobed, the lateral lobes acute, broadly triangular to subfalcate..... 8. M. BRADEORUM
gg. Lip about 15 mm. long, rather obscurely 3-lobed.
h. Leaves acuminate, 1.5 cm. or less wide, the bases tightly clasping the cylindric canes..... 19. M. EXALTATA
hh. Leaves broadly obtuse, 3.5 cm. or more wide, the persistent bases conspicuously flattened..... 22. M. INAUDITA
cc. Canes or rhizomes branching.
d. Rhizome repent, rooting freely from the bases of the caespitose leaf clusters, which are distant or terminal on the stems..... 33. M. REPENS
dd. Canes erect or pendent, not freely rooting from caespitose leaf clusters, the leaves equidistantly distributed on the stems.
e. Plants dwarf, 15 cm. or less tall.
f. Leaves coriaceous, elliptic, broadly obtuse..... 41. M. WERCKLEI
ff. Leaves fleshy, subulate-conduplicate, or rarely lanceolate, acute, never broadly obtuse..... 37. M. UNCATA
ee. Plants 30 cm. or more tall.
f. Canes slender. Leaves very short, 6 cm. or less long (usually much less)..... 17. M. DENDROBIOIDES
ff. Canes relatively stout. Leaves 10 cm. long or more.
g. Flowers conspicuously pedicellate; sepals over 15 mm. long. Column with a distinct foot..... 29. M. PARVILABIA
gg. Flowers in dense subsessile fascicles; sepals 10 mm. or less long. Column without a foot. Plants usually with an ovoid pseudobulb at the base.
h. Lip geniculate, sigmoid in profile.
hh. Lip not geniculate, not sigmoid in profile.
i. Apex of the lip 2-lobed..... 12. M. CONDUPLICATA
ii. Apex of the lip subaristate..... 30. M. PITTIERI

1. Maxillaria alba (Hook.) Lindl. Gen. & Spec. Orch. Pl. 143. 1832.

Dendrobium album Hook. Exot. Fl. *t. 142.* 1823–1827.
Broughtonia alba Spreng. Syst. Veg. 735. 1826.

Epiphytic herbs with elongate, often branching, more or less pendulous, rhizomatous stems enveloped in closely imbricating, persistent, brown, papery bracts. Pseudobulbs approximate, inserted at an acute angle on the stems and more or less imbricating, linear-elliptic, strongly ancipitous, 4–5 cm. long and 2–2.5 cm. wide, the rather oblique truncate apex with a solitary leaf. Leaves ligular, coriaceous, persistent, acuminate, 25–40 cm. long and 1.5–2 cm. wide. Inflorescences short 1-flowered scapes 3–5 cm. long from the bract axils of the flush of new growth. Flowers few to about 8, relatively small, apparently produced more or less simultaneously rather than in successive flowerings as in some of the allied species. Sepals subequal, free, spreading, creamy white, ligular, acuminate, 2–2.5 cm. long and .4–.5 cm. wide, the laterals adnate to the column foot, forming a short subacute mentum. Petals subequal to the sepals, creamy white, lanceolate, acute to acuminate, 1.8–2 cm. long and .4–.5 cm. wide. Lip concave, slightly arcuate, obscurely 3-lobed, yellow; more or less elliptic-oblanceolate, acute, when spread out, 12–15 mm. long and about 5 mm. wide, contracted at the base and articulated with the foot of the column, the lateral lobes erect, the mid-lobe about ⅓ the total length of the lip, ovate, acute, somewhat thickened; disk with an elongate, ligular, fleshy callus. Column semi-terete, lightly arcuate, 7–9 mm. long, somewhat dilated and obscurely auriculate at the apex, the base produced into a distinct foot. Anther terminal, operculate, incumbent, obscurely 2-celled.

Guatemala, Honduras, Costa Rica, Panama, Cuba, Jamaica, Trinidad, British Guiana, Surinam, Brazil, and probably other adjacent territories.

panamá: hills near Panama City, sea level, *Powell 127;* vic. Juan Diaz, sea level, *Cope s. n.* (under *Allen 3822*). chiriquí: vic. Boquete, 3800 ft., *Davidson 826;* in low woods along small streams on rocky plains about 5 miles south of Boquete, 3000 ft., *Allen 4706.*

2. Maxillaria Allenii L. Wms. in Ann. Mo. Bot. Gard. 27:282 *t. 35.* 1940.

Erect epiphytic herbs without pseudobulbs, the complanate-cylindric canes 25–40 cm. tall, the lower half to two-thirds leafless and enveloped in the coarse, closely imbricating, persistent leaf bases. Leaves 2-ranked, equidistantly distributed along the upper half to third of the stem, coriaceous, ligular, emarginate, 3.5–6.5 cm. long and 1.0–2.0 cm. wide. Inflorescences slender 1-flowered scapes produced in loose fascicles from the leaf axils. Flowers small. Sepals subequal, free, not spreading, lanceolate, acute to acuminate, 7–10 mm. long and 2–2.5 mm. wide, the laterals adnate to the foot of the column, forming a very short subacute mentum. Petals subequal to the dorsal sepal, lanceolate to oblanceolate, acute, pale yellow, 6–8 mm. long and about 2.5 mm. wide. Lip slightly concave, reddish tan to reddish orange, obscurely 3-lobed, articulated at the base with the foot of the column, 6–7 mm. long and about 3 mm. wide, lateral lobes erect, the acute apices somewhat spreading, the mid-lobe about half the total length of the lip,

the acute apex somewhat thickened and with erect margins; disk with a low, fleshy, linguiform callus. Column semi-terete, somewhat arcuate, about 4 mm. long, produced at the base into a foot. Anther terminal, operculate, incumbent, 1-celled.

Panama.

PANAMÁ: forested summit of Cerro Campana, 800–1000 m., *Allen & Fairchild 3968.* COCLÉ: wet mossy forest on Cerro Pajita, hills north of El Valle de Antón, 1200 m., *Allen & Fairchild 3941;* region north of El Valle, 1000 m., *Allen 1650, 2902, 3921.*

3. MAXILLARIA ANGUSTISEGMENTA Ames & Schweinf. in Sched. Orch. 10:86. 1930.

Erect epiphytic herbs with stout ovate to rectangular-elliptic, somewhat compressed pseudobulbs 4–6 cm. tall and 1.5–3.5 cm. wide, the bases enveloped in several imbricating papery bracts which become fibrous with age, the truncate apex of the pseudobulb with a single leaf. Leaves coriaceous, persistent, the blades oblong, acute, contracted below into an elongate, conduplicate petiole, 16–50 cm. long and 2–5 cm. wide. Inflorescences usually several, erect, 1-flowered scapes 12–15 cm. tall, enveloped in several approximate, tubular, acuminate, papery bracts. Flowers large and conspicuous. Sepals subequal, free, widely spreading, yellow, linear-lanceolate, long-acuminate, 4.5–5.5 cm. long and .5–.6 cm. wide, the laterals adnate at the base to the foot of the column, forming a short mentum. Petals subequal to the sepals, white, linear-lanceolate, acuminate, the apices incurving, 4–4.5 cm. long and .35–.5 cm. wide. Lip 3-lobed, 12–15 mm. long, contracted at the base and articulated with the foot of the column, the lateral lobes elongate, erect, the anterior margins rounded, the mid-lobe about ¼ the total length of the lip, suborbicular to subquadrate, obtuse; the disk with a fleshy ligular callus. Column semi-terete, somewhat arcuate, 8–10 mm. long, produced at the base into a foot.

Costa Rica and Panama.

CHIRIQUÍ: without definite locality, *Terry 1610;* Bajo Mono, mouth of the Quebrada Chiquero and along the Río Caldera, 1500–2000 m., *Woodson, Allen & Seibert 1010.*

Our specimens vary among themselves, none agreeing entirely with the Costa Rican type, yet they seem to form an association more readily referable to that concept than to any other species, differing from *Maxillaria ringens* in the larger flowers and more robust habit, and from *Maxillaria luteo-alba* in the much more attenuate floral segments. It seems likely that this, and many others of this association, will eventually be reduced to synonymy.

4. MAXILLARIA ANGUSTISSIMA Ames, Hub. & Schweinf. in Bot. Mus. Leafl. Harv. Univ. 3:41. 1934.

Maxillaria acutifolia Schltr. in Fedde Rep. Sp. Nov. Beih. 19:229. 1923, non Lindl.

Caespitose, usually pendulous, epiphytic herbs without pseudobulbs, the short rhizome with one to several, sometimes divaricate, clusters of long-attenuate

foliage. Leaves coriaceous, very narrow (in our specimen), 45–75 cm. long and .2–.3 cm. wide, the bases enveloped in several papery, imbricating bracts, forming a short complanate petiole. Inflorescences apparently solitary, short, 1-flowered scapes from the lower leaf axils. Sepals subequal, free, apparently not spreading (in our specimen), lanceolate, acuminate, about 2.5 cm. long and 5–6 mm. wide, the very oblique bases of the laterals adnate to the long column foot, forming a conspicuous, elongate, acuminate mentum. Petals apparently subequal to the sepals. Lip obscurely 3-lobed, concave, the slender base articulated with the column foot, the lateral lobes erect, the apical lobe spreading, about ⅓ the total length of the lip; disk with a low, fleshy, linear callus about equaling the lateral lobes in length. Column short, semi-terete, somewhat arcuate, produced at the base into a very long narrow foot.

Costa Rica and Panama.

COLÓN: summit of Cerro Santa Rita, 1200 ft., *Allen & Fairchild 5198.*

All the plants seen of this curious species have had the leaves consistently longer and narrower than in the typical Costa Rican material. The single flower of our specimen is fragmentary, and hence cannot be determined with certainty, but the plants and flowers in general aspect apparently compare better with this than with any other known species. It may be that adequate collections will prove it to be distinct.

5. MAXILLARIA ARACHNITIFLORA Ames & Schweinf. in Sched. Orch. 10:87. 1930.

Erect, caespitose, epiphytic herbs, up to about 38 cm. tall. Pseudobulbs complanate-cylindric, monophyllous, 4–5.5 cm. long and .5–1.0 cm. wide, the bases enveloped in several imbricating, sometimes foliaceous bracts. Leaves coriaceous, persistent, lanceolate, acute, 15–35 cm. long and 2.5–4.5 cm. wide, contracted below into an elongate, conduplicate petiole which is apparently continuous with the apex of the narrow pseudobulb. Inflorescences few to many erect 1-flowered scapes, 7–12 cm. tall, produced from the bases of the pseudobulbs, enveloped throughout in tubular, acuminate, papery bracts. Flowers relatively large and conspicuous. Sepals free, subequal, spreading, greenish yellow, linear-lanceolate, attenuate, 5–7.5 cm. long and .5–.6 cm. wide, the oblique bases of the laterals adnate to the column foot, forming a conspicuous acute mentum. Petals subequal to the sepals, white, erect with incurving apices, linear-lanceolate, long-acuminate, 5–6 cm. long and .4–.5 cm. wide. Lip concave, slightly arcuate, nearly entire but obscurely 3-lobed near the apex, clear yellow, oblong-ovate when spread out, 1.5–2 cm. long and .9–1.1 cm. wide, the base articulated with the foot of the column, the lateral margins erect, the apices bluntly acute, the obtuse mid-lobe somewhat thickened, with a fleshy callus on the under-side of the apex; disk with a fairly prominent, fleshy, slightly concave, linguiform callus about half the length of the lateral margins. Column short, stout, semi-terete, 6–7 mm. long, produced at the base into a very conspicuous foot which is about twice the length of the upper column.

Costa Rica and Panama.

COCLÉ: vic. El Valle de Antón, 600–1000 m., *Allen 1250;* trail to Las Minas, region north of El Valle, 1000 m., *Allen 2875.*

6. MAXILLARIA BIOLLEYI (Schltr.) L. Wms. in Ann. Mo. Bot. Gard. 28:425. 1941.

Ornithidium Biolleyi Schltr. in Fedde Rep. Sp. Nov. 9:29. 1910.
Camaridium Biolleyi Schltr. in Beih. Bot. Centralbl. 36^2:498. 1918.

Erect epiphytic herbs, 30–50 cm. tall, the stout complanate-cylindric canes enveloped below in the broad persistent leaf bases, the base of the cane often with one or more oblong-elliptic, compressed pseudobulbs, 2.5–3 cm. long and 1.5–2 cm. wide. Leaves coriaceous, spreading, 2-ranked and equidistantly distributed on the upper stem, the blades ligular, shallowly and unequally 2-lobed to acute, 7–27 cm. long and 1.5–3.5 cm. wide, the conduplicate bases closely imbricating. Inflorescences slender 1-flowered scapes, 6–9 cm. long, produced in dense fascicles from the leaf axils. Flowers small. Sepals subequal, free, spreading, white, lanceolate, acuminate, 10–12 mm. long and 3.5–4 mm. wide, the laterals somewhat obliquely inserted. Petals subequal to the sepals, rather obliquely lanceolate, acuminate, white, 9–10 mm. long and 2–3 mm. wide. Lip 3-lobed, shortly clawed at the base, red, 5–6 mm. long, the lateral lobes auriculate and erect, the mid-lobe spreading, oblong-elliptic, obtuse, about ⅔ the length of the lip; disk between the lateral lobes with a broadly obtuse, reniform, fleshy callus. Column short, stout, semi-terete, 2–2.5 mm. long, produced at the base into a very short foot.

Costa Rica and Panama.

CHIRIQUÍ: Bajo Chorro, in rain forest, 6000 ft., *Davidson 125.*

7. MAXILLARIA BRACHYBULBON Schltr. in Fedde Rep. Sp. Nov. Beih. 19:55. 1923.

Dwarf, caespitose, epiphytic herbs, 3.5–8 cm. tall, usually without pseudobulbs. Leaves coriaceous, ligular to oblanceolate, obtuse, 2–4.5 cm. long and .3–.8 cm. wide, contracted below into elongate, conduplicate petioles, the bases of which are imbricating and more or less 2-ranked. Inflorescences short, usually solitary, 1-flowered scapes produced from the base of the leaves. Flowers small, but relatively large in relation to the size of the plants. Sepals subequal, free, yellow, lanceolate, acute, 12–15 mm. long and 3–4 mm. wide, the laterals obliquely inserted on the column foot, forming a short subacute mentum. Petals subequal to the dorsal sepal, lanceolate, acuminate, yellow, 10–12 mm. long and 2–2.5 mm. wide. Lip 3-lobed near the apex, red-brown, contracted below and articulated with the column foot, the lateral margins erect, the apices acute, mid-lobe fleshy, ligular, acute, minutely papillose, about ⅓ the total length of the lip. Column short, semi-terete, somewhat arcuate, about 5 mm. long, the base produced into a short foot.

Honduras, Costa Rica, and Panama.

PANAMÁ: Cerro Campana, 1000 m., *Allen 4026.*

8. MAXILLARIA BRADEORUM (Schltr.) L. Wms. in Ann. Mo. Bot. Gard. 28:425. 1941.

Camaridium grandiflorum Ames, in Proc. Biol. Soc. Wash. 34:149. 1921.
Camaridium Bradeorum Schltr. in Fedde Rep. Sp. Nov. Beih. 19:141. 1923.
Maxillaria ampliflora C. Schweinf. in Bot. Mus. Leafl. Harv. Univ. 8:188. 1940.

Erect or pendulous, epiphytic herbs, 45–75 cm. tall, with elongate, cylindric canes, the lower portion usually with inconspicuous, distant, complanate-elliptic pseudobulbs, the internodes naked or enveloped in the persistent, imbricating leaf bases, the upper stem without pseudobulbs and with 2-ranked foliage. Leaves coriaceous, ligular-lanceolate, acute, 12–27 cm. long and 2–3.5 cm. wide; the conduplicate petioles imbricating and 2-ranked on the stem. Inflorescences erect 1-flowered scapes 6.5–8 cm. tall, enveloped in several tubular, papery, acuminate bracts. Flowers relatively large and conspicuous. Sepals free, spreading, subequal, the apices recurved, white with a central rose-red blotch, to wine-red with yellowish margins, lanceolate, acuminate to long-acuminate, 3–5 cm. long and 1.0–1.2 cm. wide, the dorsal sepal with a keel, the laterals inserted on the very short column foot barely forming an obscure mentum. Petals subequal to the sepals and similarly colored, lanceolate, acuminate to long-acuminate, 2.5–4 cm. long and 7–8 mm. wide. Lip very short, 3-lobed, rich orange, 8–10 mm. long and 12–14 mm. wide when spread out, abruptly contracted at the base into a short claw which is articulated with the foot of the column, the subfalcate, acute, lateral lobes erect, the obtuse, concave mid-lobe about $\frac{2}{5}$ the total length of the lip, the lateral margins lightly incurving; the disk with a truncate, sulcate or obscurely 3-lobed fleshy callus which about equals the lateral lobes in length. Column short, semi-terete, 6–8 mm. long, the base with a very short foot.

Costa Rica and Panama.

COCLÉ: summit of Cerro Pajita, hills north of El Valle de Antón, 1200 m., *Allen & Fairchild 3942*. CHIRIQUÍ: humid forest of the cordillera east of the Río Caldera, 2000 m., *Killip 3565;* vic. Bajo Chorro, 6000 ft., *Davidson 118*.

The species is somewhat variable in regard to the presence or absence of pseudobulbs and in the size and color of the flowers.

9. MAXILLARIA BREVIPES Schltr. in Fedde Rep. Sp. Nov. Beih. 19:302. 1923.

Dwarf, erect, epiphytic herbs up to about 8 cm. tall. Pseudobulbs clustered, ovoid-complanate, 8–10 mm. tall and 6–8 mm. wide, the bases enveloped in several imbricating papery bracts, the apices monophyllous. Leaves coriaceous, elliptic-lanceolate, acute, 4–6.5 cm. long and .8–1.2 cm. wide, contracted below into slender, elongate, conduplicate petioles. Inflorescences usually solitary 1-flowered scapes, 2–2.5 cm. tall, produced from the base of the pseudobulbs. Flowers relatively small. Sepals subequal, free, apparently not spreading, white, ovate-lanceolate, acute to subacute, 10–13 mm. long and 3–4 mm. wide, the oblique bases of the laterals adnate to the column foot, forming a short, acute

Fig. 179. *Maxillaria Camaridii*

mentum. Petals subequal to the dorsal sepal, somewhat obliquely lanceolate, acute, white, 10–11 mm. long and 2.5–3.5 mm. wide. Lip concave, elliptic-obovate, subacute when spread out, reddish brown, obscurely 3-lobed near the apex, 8–10 mm. long and 4–5 mm. wide, the cuneate base articulated with the foot of the column, the lateral margins erect, the apices rounded, the mid-lobe creamy yellow, obtuse, about ⅓ the total length of the lip; disk with a linear, obtuse, yellow callus about equaling the lateral margins in length. Column short, stout, semiterete, produced at the base into a long narrow foot.

Costa Rica and Panama.

COCLÉ: north rim of El Valle de Antón, near Cerro Turega, 650–700 m., *Woodson & Schery 201a;* mountains beyond La Pintada, 400–600 m., *Hunter & Allen 559;* mossy forest on crest of Cerro Pajita, hills north of El Valle de Antón, 1200 m., *Allen & Allen 4172.*

Possibly a dwarf form of *Maxillaria Reichenheimiana.*

10. MAXILLARIA CAMARIDII Rchb. f. in Hamb. Gartenzeit. 19:547. 1863.

Camaridium ochroleucum Lindl. in Bot. Reg. 10: *t. 844.* 1824, non *Maxillaria ochroleuca* Lodd. ex Lindl.
Cymbidium ochroleucum Lindl., Gen. & Spec. Orch. Pl. 168. 1833.
Ornithidium album Hook. in Bot. Mag. *t. 3306.* 1834, non *Maxillaria alba* (Hook.) Lindl.
Camaridium affine Schltr. in Fedde Rep. Sp. Nov. Beih. 17:72. 1922.

Epiphytic herbs with elongate, complanate-cylindric, pendulous stems, the lower portions with more or less approximate, elliptic, ancipitous, diphyllous pseudobulbs 3–7 cm. long and 1.5–3 cm. wide inserted at an acute angle, those toward the apex produced at more distant intervals; the internodes and the bases of the pseudobulbs enveloped in the persistent, chartaceous, brown, imbricating bases of the obtuse, foliaceous bracts. Leaves subcoriaceous, linear-lanceolate, obtuse, retuse, or unequally 2-lobed at the apex, 15–30 cm. long and 12–18 mm. wide, the conduplicate bases contracted into very short petioles. Inflorescences short 1-flowered scapes 4–5 cm. long, usually produced in successive pairs from the bract axils of the flush of new growth, each plant thus flowering 3 or 4 times during a given season. Flowers very fragrant, relatively large and conspicuous. Sepals subequal, free, widely spreading, somewhat concave, pure white, elliptic-oblanceolate, acute, 2.5–3.5 cm. long and 1.0–1.4 cm. wide, the laterals adnate at the base to the short column foot, forming an inconspicuous rounded mentum. Petals subequal to the sepals, widely spreading, somewhat concave, pure white, elliptic-oblanceolate, acute, 2.2–3 cm. long and 9–10 mm. wide. Lip white on the outer surface, rich yellow within, with reddish brown or reddish purple transverse lines, conspicuously 3-lobed, 10–12 mm. long and 10–12 mm. wide when spread out, contracted at the base and articulated with the foot of the column, the lateral lobes erect, rounded, the anterior margins obtuse to acute, the mid-lobe acute to suborbicular, more or less canaliculate to spreading, ⅖ to ½ the total length of the lip; disk with a linear-lanceolate, concave, yellow callus, ⅔ to ¾ the length of the lateral lobes, the obscurely tridenticulate apex of which is fleshy and glabrous,

the basal ¾ densely and conspicuously papillose. Column semi-terete, somewhat arcuate, 6–8 mm. long, pure white, with a reddish brown or deep purple blotch at the base.

Guatemala, Costa Rica, Panama, Trinidad, British Guiana, Surinam, and probably other adjacent territory.

CANAL ZONE: Río Pedro Miguel, near Paraiso, *Standley 29988*. PANAMÁ: hills east of Panama City, sea level, *Powell 7;* Río Tecúmen, *Standley 29413;* Juan Díaz, sea level, *Cope s. n.;* Cerro Campana, vic. Campana, 2000 ft., *D. Allen 5087;* San José Island, Perlas Archipelago, *Harlow 58, Johnston 206, 1403*. COCLÉ: hills south of El Valle de Antón, 800 m., *Allen 2667*.

A common and attractive species, widely distributed throughout the lowlands of our area. The flowers are produced usually in pairs in several successive flowerings lasting but a single day in each instance. The fragrance is reminiscent of that of Narcissus.

11. MAXILLARIA CHARTACIFOLIA Ames & Schweinf. in Sched. Orch. 10:92. 1930.

Erect, epiphytic herbs without pseudobulbs, the foliage distichously arranged in the form of a fan. Leaves subcoriaceous, linear-lanceolate, acuminate, 8–30 cm. long and 1.0–2.2 cm. wide, the broad, conduplicate, chartaceous bases closely imbricating and persistent. Inflorescences usually about 1–3, slender, 1-flowered scapes 6–9 cm. tall, enveloped in several papery, tubular, acuminate bracts. Flowers relatively small, dull purplish red or reddish brown. Sepals subequal, free, spreading, elliptic-lanceolate, acute, 14–18 mm. long and 5.5–7.3 mm. wide, the laterals somewhat obliquely inserted on the short column foot, forming an inconspicuous, rounded mentum. Petals subequal to the dorsal sepal, elliptic-oblanceolate, acute, 10–13 mm. long and 3.5–5 mm. wide. Lip entire or very obscurely 3-lobed, oblong-ovate, obtuse or subacute, 10–14 mm. long and 2.5–3.5 mm. wide, contracted at the base and articulated with the short column foot, the lateral margins somewhat involute, the apical lobe ovate to oblong-ovate, obtuse to subacute, spreading. Column semi-terete, somewhat arcuate, 6–7.5 mm. long, produced at the base into a short foot.

Costa Rica and Panama.

COCLÉ: vic. El Valle de Antón, 600–1000 m., *Allen 1256, 2074, 4450*.

A curious species, unlike most other Maxillarias, the plants somewhat reminiscent of a *Chondrorhyncha*. The last two collections cited have shorter and narrower leaves and somewhat smaller flowers than those of the type, but otherwise appear to be more nearly referable to this species than to any other.

12. MAXILLARIA CONDUPLICATA (A. & S.) L. Wms. in Ann. Mo. Bot. Gard. 29:348. 1942.

Ornithidium conduplicatum Ames & Schweinf. in Sched. Orch. 8:66, *t. 5*. 1925.

Stout, erect, epiphytic herbs with cylindric, ascending stems apparently often branching and enveloped in 2-ranked foliage; the base of the cane with one or

more stout, ovoid, monophyllous pseudobulbs, in our specimen 5.5 cm. tall and 3.5 cm. wide. Mature leaves absent in our specimen, but apparently large, numerous and ligular, the upper stem covered by the broad, coarse, complanate, 2-ranked, imbricating, persistent bases. Inflorescences short 1-flowered scapes about 2.5 cm. long, produced in dense fascicles from the leaf axils. Flowers small. Sepals subequal, free, apparently not spreading, elliptic-lanceolate, acute, about 6 mm. long and 2–2.5 mm. wide, the laterals somewhat oblique and concave at the base. Petals subequal to the dorsal sepal, elliptic-obovate, acute, about 5 mm. long and 2 mm. wide. Lip canaliculate, with a deep median constriction, more or less subquadrate and 4-lobed when spread out, about 4 mm. long and 2.6 mm. wide, the narrowed base adnate to the base of the column, the lateral lobes rounded, erect in natural position, the mid-lobe suborbicular, conspicuously emarginate at the apex, the lateral concave, rounded lobules erect, the median constriction with a transverse, fleshy callus. Column very short, stout, about 1.75 mm. long.

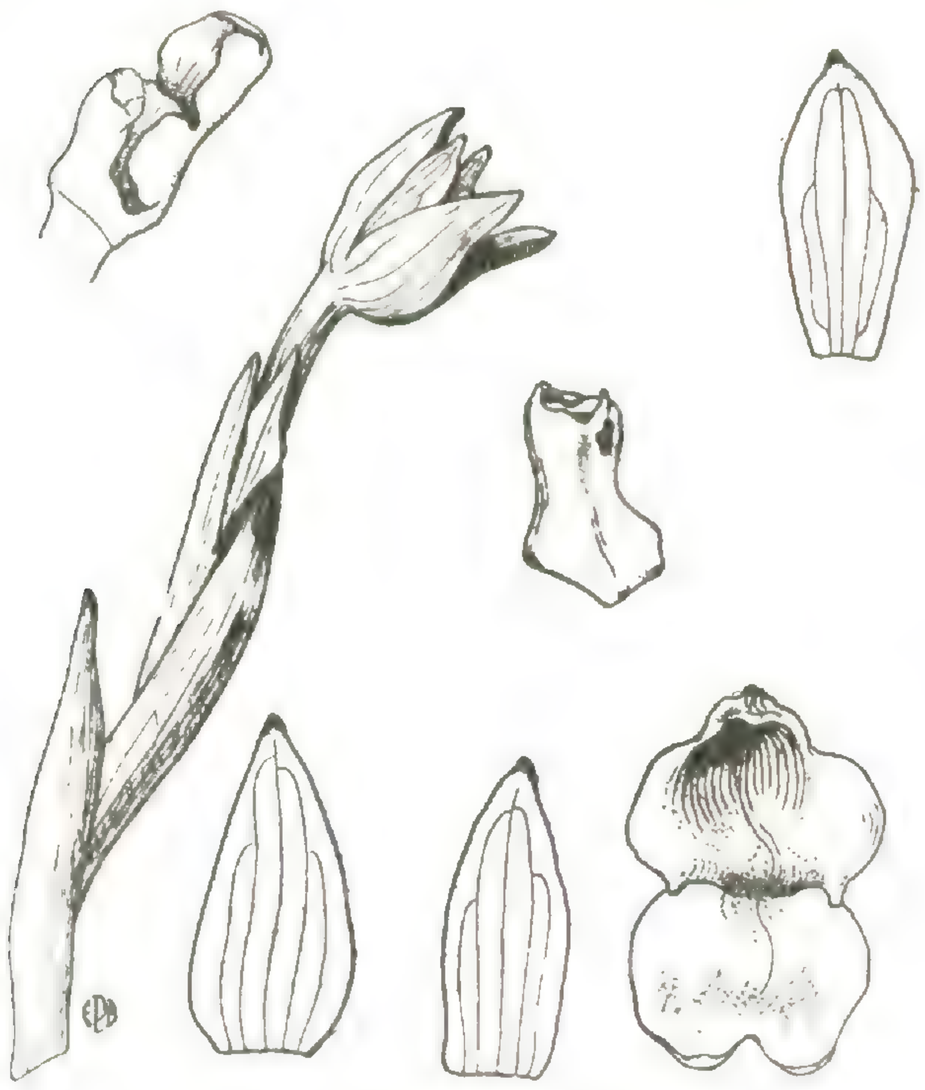


Fig. 180. *Maxillaria conduplicata*

Panama.

CHIRIQUÍ: Palo Alto Hill, 4000–5000 ft., *Powell 341*.

Known only from the type collection.

13. MAXILLARIA CONFUSA Ames & Schweinf. in Sched. Orch. 8:57. 1925.

Small, erect, epiphytic herbs up to about 25 cm. tall, with clustered, elliptic-oblong, compressed, monophyllous pseudobulbs 12–18 mm. tall and 8–12 mm. wide, the bases enveloped in several imbricating bracts, the upper pair of which is usually foliaceous. Leaves coriaceous, grayish green, ligular to elliptic-lanceolate, acute, 7–16 cm. long and 2–3.5 cm. wide, contracted below into elongate, slender, conduplicate petioles. Inflorescences usually 6–8 slender, 1-flowered scapes 3–4 cm. long, produced from the base of the pseudobulbs. Flowers of moderate size, but large in relation to the size of the plants. Sepals subequal, free, spreading, white, linear-lanceolate, abruptly acute, 17–20 mm. long and 4–5 mm. wide, the oblique bases of the laterals inserted on the elongate column foot, forming a conspicuous acuminate mentum. Petals subequal to the dorsal sepal, white, from an oblique base lanceolate-acuminate, 15–17 mm. long and 4–5 mm. wide. Lip canaliculate, reddish brown, obscurely 3-lobed near the apex, oblong-

obovate, about 12 mm. long and 6 mm. wide when spread out, contracted at the base and articulated with the foot of the column, the lateral margins erect, the apices rounded, mid-lobe ovate, acute, about ¼ the total length of the lip, conspicuously thickened and with a tubercle on the under-surface of the apex; disk with a fleshy linguiform callus, about ⅔ the length of the lateral margins. Column short, stout, semi-terete, somewhat arcuate, produced at the base into a long narrow foot.

Costa Rica and Panama.

VERAGUAS: forested slopes of Cerro Tuté, region west of Santa Fé, 2500 ft., *Allen & Fairchild 4405*.

It seems quite possible that this species, as well as *Maxillaria brevipes* and M. *arachnitiflora*, may prove to be but well-marked varieties of *Maxillaria Reichenheimiana*.

14. MAXILLARIA CRASSIFOLIA (Lindl.) Rchb. f. in Bonplandia 2:16. 1854.

Epidendrum sessile Swartz, Prodr. Veg. Ind. Occ. 122. 1788, non *Maxillaria sessilis* Lindl.
Heterotaxis crassifolia Lindl. in Bot. Reg. 12: *t. 1028*. 1826.
Dicrypta Baueri Lindl. Gen. & Spec. Orch. Pl. 44. 1830.
Dicrypta crassifolia Lindl. ex Loud. Hort. Brit. Suppl. 3:536. 1839.
Maxillaria sessilis Fawcett & Rendle, Fl. Jam. 1:120. 1910, non Lindley.
Maxillaria gatunensis Schltr. in Fedde Rep. Sp. Nov. Beih. 17:68. 1922.

Erect, caespitose, epiphytic herbs averaging about 30 cm. tall. Leaves fleshy, linear-lanceolate, obtuse to acute, 6–35 cm. long and 1–3.8 cm. wide, the conduplicate bases imbricating and forming a short, more or less complanate petiole, sometimes enveloping an inconspicuous, poorly developed, oblong, monophyllous pseudobulb, all but the leaf of the pseudobulb actually being foliaceous bracts. Inflorescences usually short, solitary, 1-flowered scapes, nearly sessile in the upper bract axils. Flowers of moderate size. Sepals subequal, free, spreading, usually yellow or pale yellow, lanceolate, acute, 16–20 mm. long and 5–6 mm. wide, the dorsal sepal somewhat concave, the laterals adnate to the column foot, forming a short, rounded mentum. Petals usually yellow, subequal to the dorsal sepal, linear-lanceolate to oblanceolate, acute, 14–17 mm. long and 3–4 mm. wide. Lip nearly entire or obscurely 3-lobed, yellow with red spots to dark red, concave, 12–14 mm. long and 5–7 mm. wide when spread out, contracted at the base and articulated with the column foot, lateral margins erect, the mid-lobe about ⅓ to ½ the total length of the lip, somewhat thickened and minutely papillose; the disk with a fleshy, thickened keel. Column elongate, semi-terete, somewhat arcuate, 7–9 mm. long, produced at the base into a short foot.

Mexico, Guatemala, British Honduras, Honduras, Costa Rica, Panama, Colombia, Venezuela, Brazil, Florida, Cuba, Jamaica, Hispaniola and probably other adjacent areas.

CANAL ZONE: Gatún Lake, sea level, *Powell 207*. PANAMÁ: San José Island, Perlas Archipelago, *Johnston 273, 1275-A*. CHIRIQUÍ: without definite locality, 4000 ft., *Powell*

118. BOCAS DEL TORO: without definite locality, *von Wedel 477.* DARIÉN: vic. Pinogana, Río Tuira, 20 m., *Allen 917.*

A vèry common, weedy species widely distributed throughout the lowlands of our area.

15. MAXILLARIA CTENOSTACHYA Rchb. f. in Gard. Chron. 39. 1870.

Maxillaria ctenostachys Rchb. f. ex Schltr. in Beih. Bot. Centralbl. 36^2:495. 1918.
Camaridium arachnites Schltr. in Fedde Rep. Sp. Nov. Beih. 17:73. 1922.
Camaridium stenostachys Schltr. loc. cit. 19:238. 1923.

Elongate, slender, erect or pendulous, epiphytic herbs. Pseudobulbs elliptic, ovoid, complanate, rugose, tapering, diphyllous, those at the base of the plant clustered, 3.5–6.5 cm. tall and 2.5–4 cm. wide, those on the upper branching stem becoming very distant and inserted at an acute angle, 2.5–5 cm. tall and 1.5–2 cm. thick, the bases provided with several elongate, foliaceous bracts; the long internodes closely enveloped in long, acuminate, persistent, papery bracts. Leaves coriaceous, linear-lanceolate, acute, 15–35 cm. long and 1–2.5 cm. wide, contracted below into short conduplicate petioles. Inflorescences usually many short, slender, 1-flowered scapes 1.5–2 cm. long, from the bract axils of the distichous flush of new growth, which at flowering time much resembles the stem of a *Lockhartia* in vegetative appearance. Flowers relatively large, most or all being produced simultaneously, the flowering habit reminiscent of that of *Maxillaria alba.* Sepals subequal, free, more or less spreading, white or pale yellow, lanceolate, long-acuminate, 2.5–4 cm. long and .4–.5 cm. wide; the laterals adnate to the column foot, forming a short, rounded mentum. Petals subequal to the sepals, white or pale yellow, rather obliquely elliptic-lanceolate, long-acuminate, 2–3 cm. long and .3–.5 cm. wide. Lip conspicuously 3-lobed, white or pale yellow, the inner surface with brown or tan markings, 8–12 mm. long and 6–8 mm. wide when spread out, contracted at the base and articulated with the foot of the column, lateral lobes erect in natural position, the anterior margins acute, mid-lobe ovate, acute, about ½ the total length of the lip, the apex reflexed and somewhat thickened; disk with 5 erect, parallel keels, about ¾ the length of the lateral lobes, the central 3 of which are rounded at the apex and conspicuously thickened. Column semi-terete, somewhat arcuate, 4–6 mm. long, produced at the base into a short foot.

Costa Rica and Panama.

CHIRIQUÍ: Río Caldera, 4500 ft., *Powell 210.*

16. MAXILLARIA CUCULLATA Lindl. in Bot. Reg. 26: *t. 12.* 1840.

Maxillaria meleagris Lindl. loc. cit. 30: Misc. 3. 1844.
Maxillaria Lindeniana Rich. & Gal. in Ann. Sci. Nat. Bot. III, 3:24. 1845.
Maxillaria obscura Linden & Rchb. f. in Rchb. Beitr. Orch. Centr.-Amer. 31. 1866.
Maxillaria puncto-striata Rchb. f. in Linnaea 41:28. 1877.

Erect, epiphytic herbs with clustered, oblong-ovoid to elliptic-ovoid, compressed, rugose, monophyllous pseudobulbs 2.5–4 cm. tall and 1.5–2.5 cm. wide, the bases enveloped in several imbricating, papery bracts. Leaves coriaceous, acute, or retuse and obscurely 2-lobed at the apex, 15–30 cm. long and 1.5–2 cm. wide, contracted below into a conduplicate petiole. Inflorescences usually 3–4 short to elongate, 1-flowered scapes from the base of the pseudobulbs, enveloped in numerous, often spreading, conspicuous, tubular, papery, acuminate bracts. Flowers of moderate size, dark reddish or purplish brown with a maroon lip, or with yellow sepals and petals which may be marked with varying amounts of the darker color. Sepals free, subequal, spreading, lanceolate to elliptic-lanceolate, acute, 1.8–2.2 cm. long and .4–.6 cm. wide, the laterals adnate to the foot of the column, forming a short, subacute mentum. Petals lanceolate, acute, 1.5–1.8 cm. long and .4–.6 cm. wide. Lip conspicuously 3-lobed, 1.4–1.6 cm. long and .6–.8 cm. wide when spread out, contracted at the base and articulated with the foot of the column, the lateral lobes short, conspicuously erect in natural position, the mid-lobe elliptic-lanceolate to elliptic-ovate, acute to subacute, about ⅔ the total length of the lip, the apex thickened, with a fleshy keel on the under-surface; disk with a broad, obtuse, fleshy callus about equaling the lateral lobes in length. Column short, stout, somewhat arcuate, rather dilated at the apex, produced at the base into a foot.

Mexico, Guatemala, Nicaragua, Costa Rica, Panama, and probably adjacent territories.

CHIRIQUÍ: Bajo Chorro, in rain forest, 6000 ft., *Davidson 115;* in woods on Llano del Volcán, 1500 m., *Allen 3504.*

17. MAXILLARIA DENDROBIOIDES (Schltr.) L. Wms. in Ann. Mo. Bot. Gard. 27:283. 1940.

Camaridium dendrobioides Schltr. in Beih. Bot. Centralbl. 36^2:415. 1918.
Camaridium Jimenezii Schltr. loc. cit. 416. 1918.
Camaridium simile Schltr. in Fedde Rep. Sp. Nov. Beih. 19:239. 1923.

Slender, erect or pendulous, epiphytic herbs without pseudobulbs, 30–45 cm. tall, the stems usually branching, the lower portions enveloped in the closely imbricating, papery leaf bases; the foliage of the apex 2-ranked. Leaves spreading, coriaceous, ligular, the apices usually retuse or rather unequally 2-lobed, very variable in size, 1–6 cm. long and .25–1.0 cm. wide (in our specimens 1.5–2 cm. long and about .3 cm. wide), the conduplicate bases closely imbricating and persistent, enveloping the stems. Inflorescences short, slender, 1-flowered scapes 10–15 mm. long, produced from the leaf axils. Flowers small. Sepals free, subequal, apparently not spreading, lanceolate, acute or obtuse, 9–11 mm. long and 2–2.5 mm. wide, the laterals somewhat obliquely inserted on the column foot, forming a short, rounded mentum. Petals subequal to the dorsal sepal, rather obliquely elliptic-oblanceolate, obtuse or shortly acute, 7–8.5 mm. long and 2–2.5 mm. wide. Lip obscurely 3-lobed, about 7.5 mm. long and 3.5 mm. wide when

spread out, contracted at the base and articulated with the column foot, the lateral lobules or margins rounded, erect in natural position, the mid-lobe ovate to ligular, obtuse, about ½ the total length of the lip; disk with 3 parallel, thickened nerves, about ½ the length of the lateral margins. Column semi-terete, about 3.5 mm. long, produced at the base into a short foot.

Costa Rica and Panama.

CHIRIQUÍ: vic. Bajo Chorro, in heavy rain forest, 6000 ft., *Davidson 240.*

18. MAXILLARIA DIUTURNA Ames & Schweinf. in Sched. Orch. 8:58. 1925.

Erect or pendent, epiphytic herbs with elliptic-oblong to elliptic-ovate, strongly ancipitous, monophyllous pseudobulbs 2–3 cm. long and .1–.2 cm. wide, rather distant and inserted at an acute angle on the stems; the internodes and bases of the pseudobulbs enveloped in closely imbricating, persistent bracts the upper pair of which is foliaceous. Leaves persistent, coriaceous, ligular to elliptic-lanceolate, acute or minutely and unequally 2-lobed, 6–15 cm. long and 1.2–3 cm. wide, contracted below into short, conduplicate petioles. Inflorescences short, slender, 1-flowered scapes, apparently produced singly in succession from the bract axils of the flush of new growth. Flowers pseudo-campanulate, of moderate size. Sepals subequal, free, not spreading, bright yellow or sometimes reddish yellow on the outer surfaces, 12–14 mm. long and 5–6 mm. wide, ovate-lanceolate, acute, concave, with a low central keel, the laterals adnate to the column foot forming a prominent, rounded mentum. Petals elliptic-ovate, acute, bright yellow, 10–12 mm. long and 6–7 mm. wide. Lip entire, bright yellow with scarlet markings, oblong-pandurate, 10–12 mm. long and 5–6 mm. wide when spread out, somewhat contracted at the base and articulated with the column foot, lateral margins somewhat erect in natural position, the apex truncate, obscurely emarginate and 2-lobed, the lobules somewhat erect in natural position; the disk with a linear to oblong, obtuse, fleshy callus. Column semi-terete, somewhat arcuate, 5–6 mm. long, produced at the base into a foot.

Costa Rica and Panama.

PANAMÁ: cloud forest on the summit of Cerro Campana, 3000 ft., *Allen 5183.* COLÓN: Cativo-Porto Bello trail, sea level, *Powell 376.* COCLÉ: vic. La Mesa, region north of El Valle de Antón, 1000 m., *Allen 2306, 2935.*

19. MAXILLARIA EXALTATA (Kränzl.) C. Schweinf. in Bot. Mus. Leafl. Harv. Univ. 11:272. 1945.

Camaridium exaltatum Kränzl. in Engler's Bot. Jahrb. 37:386. 1906.

Tall, erect, epiphytic herbs, the cylindric, sometimes branching stems 60–75 cm. tall, apparently entirely without pseudobulbs, the lower portions enveloped in the closely imbricating, persistent, chartaceous leaf bases which ultimately weather to loose fibers, the upper stem with 2-ranked foliage. Leaves coriaceous, linear-lanceolate, acuminate, 9–25 cm. long and .8–1.5 cm. wide, the broad, conduplicate bases imbricating and equidistantly distributed on the stem. Inflores-

cences usually several, slender, 1-flowered scapes 5–6 cm. long, produced from the upper leaf axils. Flowers of moderate size. Sepals free, subequal, spreading, pale pinkish tan (in our specimens), the dorsal sepal linear-lanceolate, acute, with a central keel, 2–2.5 cm. long and .35–5 cm. wide, the laterals ligular, acute, 2.3–2.8 cm. long and .5–.7 cm. wide, the bases rather oblique and adnate to the column foot, forming a prominent acute mentum. Petals linear-lanceolate, acute, pale pinkish tan (in our specimens), 2–2.2 cm. long and .3–.4 cm. wide. Lip 3-lobed near the apex, reddish-brown, 13–15 mm. long and 6–8 mm. wide when spread out, contracted at the base and articulated with the column foot, lateral lobes erect in natural position, the anterior margins subacute and somewhat projecting, the mid-lobe ovate, abruptly acute, about ¼ the total length of the lip, conspicuously thickened and minutely papillose, with a prominent tubercle on the underside of the apex; the disk with a ligular, rather concave, obtuse callus, about ¾ the length of the lateral lobes, the apex rather conspicuously thickened. Column short, stout, semi-terete, produced at the base into a long foot.

Panama and Peru.

COCLÉ: mossy forest on the crest of Cerro Pajita, hills north of El Valle de Antón, 1200 m., *Allen & Fairchild 3945*.

This collection represents a tremendous extension of range for this rather poorly known Peruvian species. Our specimens match the excellent photograph of the type and the type description in the Ames Herbarium almost exactly, even to the size of the floral parts, which is remarkable in view of the wide separation of the areas of collection. It is of course to be expected that the species also exists in Colombia and Ecuador, and will eventually be collected there.

20. MAXILLARIA FRIEDRICHSTHALII Rchb. f. in Bot. Zeit. 10:858. 1852.

Maxillaria aciantha Rchb. f. loc. cit. 1852.
Lycaste aciantha Rchb. f. in Bonplandia 3:216. 1855.
Maxillaria turialbae Schltr. in Beih. Bot. Centralbl. 36^2:414. 1918.
Maxillaria rhodosticta Kränzl. in Fedde Rep. Sp. Nov. 24:223. 1928.

Erect or semi-pendent, epiphytic herbs with complanate, elliptic-oblong, rugose pseudobulbs 1.5–5 cm. tall and 7–15 mm. wide, approximate and inserted at an acute angle on the usually arching rhizome; the short internodes and bases of the pseudobulbs enveloped in the persistent, chartaceous bases of the closely imbricating bracts, the upper pair of which is usually foliaceous. Leaves coriaceous, 2–3 (very rarely 1 or 4) from the apex of the pseudobulbs, ligular, the apex obscurely and unequally 2-lobed, 3.5–18 cm. long and .7–1.5 cm. wide, contracted below into very short, conduplicate petioles. Inflorescences 1 to several, often loosely fasciculate, 1-flowered scapes 1.8–4 cm. long, produced from the base of the mature pseudobulb, the peduncles closely enveloped in numerous broad, acute, imbricating, chartaceous bracts. Flowers small to relatively large, the size apparently correlated with the size of the plant. Sepals subequal, free, not spread-

ing, linear-lanceolate, acute to acuminate, 1.5–3 cm. long and .3–.6 cm. wide, greenish yellow to greenish lavender, the laterals adnate to the column foot, form-

Fig. 181. *Maxillaria Friedrichsthalii*

ing a short, acute mentum. Petals lanceolate to linear-lanceolate, acute to acuminate, greenish yellow, 1.2–2.5 cm. long and .2–.3 cm. wide. Lip entire, linear-oblanceolate, obtuse to subacute, canaliculate, 1.2–2.5 cm. long and .3–.6 cm. wide, usually pale yellowish green, the long narrow base articulated with the foot of the column, the lateral margins somewhat erect, the apex conspicuously thickened, usually dark maroon to nearly black; the disk with a rather obscure, yellow central keel, which extends from the base about $\frac{2}{5}$ the total length of the lip. Column elongate, semi-terete, somewhat arcuate, 8–20 mm. long, produced at the base into a short foot.

Mexico, British Honduras, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, and probably adjacent South America.

CANAL ZONE: Barro Colorado Island, *Shattuck 543*. PANAMÁ: vic. Paja, sea level, *Powell 3210;* Cerro Campana, vic. Campana, 800 m., *Allen 4025*. COCLÉ: vic. El Valle de Antón, 600–1100 m., *Allen 1254, 1257, 3992;* Bismarck, 2000–3000 ft., *Williams 444*. CHIRIQUÍ: without definite locality, 4000–5000 ft., *Powell 3516;* Bajo Mono, 4500 ft., *Davidson 524*.

A very common species, widely distributed throughout the lowlands and intermediate highlands of our area.

21. MAXILLARIA FULGENS (Rchb. f.) L. Wms. in Ann. Mo. Bot. Gard. 28:425. 1941.

Ornithidium fulgens Rchb. f. Beitr. Orch. Centr.-Amer. 76. 1866.

Erect, epiphytic herbs 40–75 cm. tall, with elongate, often branching, cylindric, woody canes usually arising from a basal cluster of a few stout, ovoid, fleshy pseudobulbs 3.5–4 cm. tall and 2–3 cm. wide; the long internodes or basal portions of the stems closely enveloped in the persistent, imbricating leaf bases, or becoming naked after these have weathered away; the apex of the cane with 2-ranked foliage. Leaves coriaceous, linear-lanceolate, acute, 12–38 cm. long and 1.5–3 cm. wide, forming a compact, distichous fascicle at the apex of the stems, portions of which are often still in evidence at the earlier nodes along the more elongate canes, the conduplicate leaf bases sometimes enveloping a small, poorly developed pseudobulb. Inflorescences usually about 15–30 slender, 1-flowered scapes, 1.5–3 cm. tall, in dense subsessile fascicles from the lower leaf axils. Sepals rather fleshy, subequal, free, not spreading, broadly ovate, acute, concave, reddish orange, 7–8 mm. long and 3–3.5 mm. wide, the laterals adnate to the somewhat produced base of the column, forming a short, rounded mentum. Petals lanceolate, acute, 5–6 mm. long and about 2.5 mm. wide, suffused reddish orange shading to yellow at the base. Lip entire, bright yellow or orange, 4–4.5 mm. long and 1.5–2 mm. wide, geniculate and more or less sigmoid in profile, the orbicular basal half deeply concave or subsaccate, adnate to the base of the column, the strongly reflexed apical half elliptic-oblong, obtuse, rather fleshy, with thin, erect, often somewhat undulant margins, the apex becoming rather shallowly emarginate, with a short, acute, fleshy, carinate projection on the under-surface. Column semiterete, somewhat arcuate, bright yellow, 2.5–3 mm. long, the base without a foot.

Costa Rica and Panama.

COCLÉ: region north of El Valle de Antón, vic. La Mesa and La Loma del Tigre, about 3000 ft., *Allen 2256, 2388, 3779*. CHIRIQUÍ: Caramilla, 5000 ft., *Powell 283*.

A frequent, attractive species of the wet highland forests of Coclé and Chiriquí provinces.

22. MAXILLARIA INAUDITA Rchb. f. Beitr. Orch. Centr.-Amer. 76. 1866.

Robust, erect or pendulous, epiphytic herbs 45–60 cm. tall, the elongate

cylindric canes provided with distichous, spreading foliage at the apex, the basal portions enveloped in the broad, complanate, persistent, imbricating leaf bases; the plants seemingly without pseudobulbs but sometimes with 1 or more elliptic-oblong, strongly ancipitous, monophyllous pseudobulbs up to 8 cm. tall and 4.5 cm. wide at the base of the leafy cane. Leaves coriaceous, ligular to elliptic-lanceolate, broadly obtuse, 15–25 cm. long and 3.5–4.5 cm. wide, contracted at the base into narrow conduplicate petioles, the broader rugose bases persistent and equidistantly distributed on the stems. Inflorescences short 1-flowered scapes 4–5 cm. long, produced from the axils of the leaves. Flowers relatively large and conspicuous. Sepals subequal, free, spreading, lanceolate, acuminate, white, 2.5–4 cm. long and 6–8 mm. wide, the laterals adnate to the column foot, forming an inconspicuous, rounded mentum. Petals lanceolate, acuminate, white, 2.2–3 cm. long and .4–.5 cm. wide. Lip rather obscurely 3-lobed, ovate, obtuse to subacute when spread out, 1.5 cm. long and 1 cm. wide, contracted at the base into a short claw which is articulated with the foot of the column, the lateral lobes white, erect in natural position, the mid-lobe ovate, obtuse to subacute, yellow, about ⅓ the total length of the lip, separated from the lateral lobes by plicate folds; the disk with a concave, ligular, obtuse callus which is about ¾ the length of the lateral lobes. Column semi-terete, somewhat arcuate, 6–8 mm. long, produced at the base into a short foot.

Costa Rica and Panama.

VERAGUAS: forested slopes of Cerro Tuté, region west of Santa Fé, 3000 ft., *Allen & Fairchild 4338*.

23. MAXILLARIA LONGIPETIOLATA Ames & Schweinf. in Sched. Orch. 8:61. 1925.

Erect, epiphytic herbs about 23 cm. tall, with elliptic-ovoid, compressed, somewhat finely wrinkled monophyllous pseudobulbs 2.5 cm. tall and 1.5 cm. wide, which apparently are approximate on an abbreviated rhizome, the bases enveloped in several papery bracts which become fibrous with age. Leaves subcoriaceous, linear-lanceolate, acuminate, 16 cm. long and 2 cm. wide, contracted below into an elongate, slender, conduplicate petiole. Inflorescences apparently short, solitary, 1-flowered scapes from the base of the pseudobulbs. Flowers of moderate size. Sepals subequal, free, spreading, oblong-lanceolate, acute, Indian red, 16–18 mm. long and 5.5–5.8 mm. wide. Petals subequal to the dorsal sepal, Indian red, linear-lanceolate, rather obliquely acute, 1.5–2.5 cm. long and about 3 mm. wide. Lip conspicuously 3-lobed, dark maroon, about 1.4 cm. long and .8 cm. wide when spread out, contracted at the base and articulated with the foot of the column, the lateral lobes erect in natural position, the acute apices spreading, the mid-lobe ligular, about ½ the total length of the lip, the rounded apex lightly retuse; the disk with a linear-lanceolate callus about ⅔ the length of the lateral lobes, the obtuse apex rather fleshy. Column semi-terete, somewhat arcuate, about 7 mm. long, produced at the base into a short foot. Anther yellow.

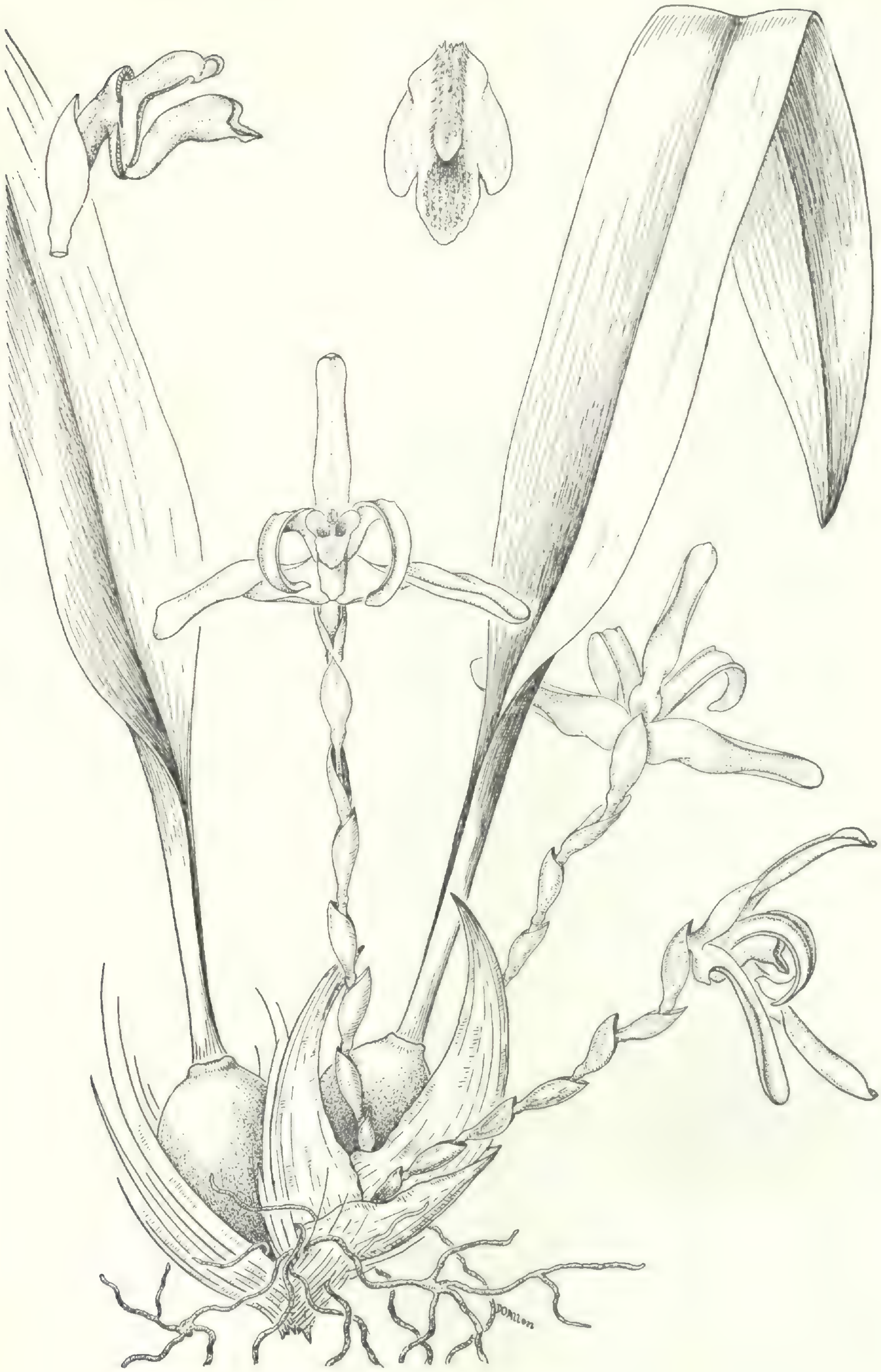


Fig. 182. *Maxillaria luteo-alba*

Panama.

PANAMÁ: hills east of Corozal, sea level, *Powell 307*.

Known only from the type collection.

24. MAXILLARIA LUTEO-ALBA Lindl. Orch. Linden. 20. 1846.

Maxillaria luteo-grandiflora Hort. in Flor. Mag. 10: *t. 559*. 1871.

Erect, epiphytic herbs with stout, oblong-ovoid to elliptic-ovoid, somewhat compressed, monophyllous pseudobulbs 3–5 cm. tall and 2–3 cm. wide, the bases enveloped in several long, papery, imbricating bracts which become fibrous with age. Leaves coriaceous, linear-lanceolate to elliptic-lanceolate, acute, 25–50 cm. long and 2.5–4 cm. wide, contracted below into short or elongate, conduplicate petioles. Inflorescences usually about 3 erect, 1-flowered scapes 9–14 cm. long, produced from the bases of the pseudobulbs, enveloped in several papery, acute, tubular bracts. Flowers conspicuous, the largest of the genus in Panama. Sepals subequal, free, widely spreading, ligular, broadly obtuse, white on the outer surfaces and pale yellow within, 4–5 cm. long and 1.0–1.2 cm. wide, the laterals adnate to the column foot, forming a prominent, acute mentum. Petals ligular, shortly subacute, the apices incurving in natural position, white without and pale yellow within, 3.5–4 cm. long and .5–.7 cm. wide. Lip conspicuously 3-lobed, deep yellow, margined white, about 2.5 cm. long and 1.8 cm. wide when spread out, contracted at the base and articulated with the foot of the column, the lateral lobes erect in natural position, the rounded apices somewhat projecting, mid-lobe ovate, obtuse, about ⅓ the total length of the lip; the disk with a linguiform, laterally bicarinate, acute callus, about ⅔ the length of the lateral lobes. Column semi-terete, somewhat arcuate, about equaling the length of the lateral lobes of the lip.

Costa Rica, Panama, Colombia, and Ecuador.

COCLÉ: hills north of El Valle de Antón, crest of Cerro Pajita and La Loma del Tigre, 3000–3200 ft., *Allen 2870, 3817, 4192*.

A common, large-flowered, attractive species of the high rainy hills north of El Valle, and to be expected in other similar situations throughout our range.

25. MAXILLARIA MALEOLENS Schltr. in Fedde Rep. Sp. Nov. Beih. 19:233. 1923.

Erect, epiphytic herbs 30–45 cm. tall, with approximate or solitary, strongly ancipitous, monophyllous, oblong-elliptic pseudobulbs 4.5–8 cm. tall and 2–3.5 cm. wide, the bases enveloped in 3–4 complanate, imbricating, foliaceous bracts. Leaves coriaceous, ligular, broadly obtuse, 15–45 cm. long and 2.5–5 cm. wide, contracted below into conduplicate petioles, the complanate-conduplicate bases distichously arranged in the form of an open fan. Inflorescences usually solitary, 1-flowered scapes 5–8 cm. long, produced from the upper bract axils. Flowers of moderate size, fragrant. Sepals subequal, free, spreading, yellow, elliptic-lanceolate, acute, 2–2.5 cm. long and .8–1.0 wide, the laterals rather obliquely

inserted on the column foot, forming a short, rounded mentum. Petals yellow, ligular, the apices obliquely acute, 18–20 mm. long and 4–5 mm. wide. Lip rather obscurely 3-lobed, reddish brown to rich purple throughout, or sometimes with the lateral lobes yellow, 2–2.3 cm. long and 1–1.2 cm. wide when spread out, contracted at the base and articulated with the foot of the column, the lateral lobes or margins rounded, erect in natural position, the mid-lobe ovate, obtuse, rather fleshy, about ⅓ the total length of the lip, reflexed at the apex; the disk with a narrow, thickened, central nerve, about equaling the lateral lobes in length. Column semi-terete, somewhat arcuate, 12–15 mm. long, produced at the base into a foot.

Honduras, Costa Rica, and Panama.

CANAL ZONE: Gatún Lake, sea level, *Powell 276.* COCLÉ: region north of El Valle de Antón, 3000 ft., *Fairchild s. n.* (under *Allen 2932*).

26. MAXILLARIA MINOR (Schltr.) L. Wms. in Amer. Orch. Soc. Bull. 10:273. 1942.

Camaridium minus Schltr. in Beih. Bot. Centralbl. 36^2:417. 1918.

Erect, epiphytic herbs with slender, branching stems provided with small, very distant, suborbicular, monophyllous, compressed pseudobulbs 6–15 mm. long and 6–15 mm. wide, the bases covered by 2–3 conspicuous, foliaceous bracts, the long internodes very closely enveloped in complanate, imbricating, acuminate, papery sheaths. Leaves subcoriaceous, lanceolate to elliptic-lanceolate, acute, 3.5–15 cm. long and 1–2 cm. wide, contracted below into slender, conduplicate petioles. Inflorescences several very short, 1-flowered scapes 5–10 mm. long, apparently produced simultaneously from the bract axils of the flush of new growth. Flowers very small, often enveloped in 2 glumaceous bracts. Sepals subequal, free, not spreading, concave, oblong-lanceolate, acute to subacute, about 4 mm. long and 2 mm. wide, the laterals adnate to the base of the column, forming a rounded, conspicuous mentum. Petals subequal to the dorsal sepal, ligular, obtuse, about 3 mm. long and 1.5 mm. wide. Lip fleshy, 3-lobed, about 3 mm. long, articulated with the base of the column, the lateral lobes rounded, erect, on either side of a basal concavity which has a short, ligular, fleshy callus, the mid-lobe ovate, subacute, nearly ½ the total length of the lip, the basal constriction below the lateral lobes with a transverse, semicircular thickening. Column short, stout, the lateral margins thickened toward the obscurely produced base.

Costa Rica and Panama.

COCLÉ: mossy forest on summit of Cerro Pajita, hills north of El Valle de Antón, 1100 m., *Allen 3991.*

27. MAXILLARIA NEGLECTA (Schltr.) L. Wms. in Ann. Mo. Bot. Gard. 29:348. 1942.

Ornithidium anceps Rchb. f. Beitr. Orch. Centr.-Amer. 75. 1866, non *Maxillaria anceps* A. & S.
Ornithidium neglectum Schltr. in Fedde Rep. Sp. Nov. Beih. 19:242. 1923.

Fig. 183. *Maxillaria neglecta*

Erect or pendulous, epiphytic herbs, of very variable vegetative habit, usually with elongate, often branching rhizomes. Pseudobulbs monophyllous, ligular to suborbicular, strongly ancipitous to very thick and fleshy, 1.5–4.5 cm. long and .5–1.5 cm. wide, approximate to very distant, inserted at an acute angle on the stems, the long cylindric internodes and the bases enveloped in closely imbricating, papery bracts. Leaves subcoriaceous, ligular, acute, 6–18 cm. long and 1.2–2.5 cm. wide, the bases contracted into very short conduplicate petioles. Inflorescences very short, 1–flowered scapes, produced in dense subsessile fascicles from the bases of the mature pseudobulbs. Flowers small, usually enveloped in 2 glumaceous bracts. Sepals free, apparently not spreading, concave, yellow or white, about 6 mm. long, the dorsal sepal elliptic-ovate, acute, the laterals broadly rhombic with oblique, acute apices, the oblique bases forming an acute or rounded, conspicuous mentum. Petals subequal to the dorsal sepal, oblong-ligular, subacute, about 4.5 mm. long, similarly colored with the sepals. Lip yellow, about 6 mm. long and 3 mm. wide when spread out, geniculate in profile, the long narrow base continuous with the base of the column, the limb dilated and conspicuously 3-lobed near the apex, the obliquely triangular lateral lobes erect, joined below the apices by a narrow transverse callus, the mid-lobe rather fleshy, triangular to broadly ovate, acute to obtuse, inserted at an abruptly deflexed angle below the apices of the lateral lobes. Column short, about 1.7 mm. long, the base continuous with the claw of the lip.

Honduras, Nicaragua, Costa Rica, and Panama.

CANAL ZONE: hills north of Frijoles, *Standley 27669*. PANAMÁ: hills east of Panama City, sea level, *Powell 324*. COLÓN: Río Pequení, upper Madden Lake region, 200 ft., *Fairchild s. n.*; Cerro Santa Rita, 1200 ft., *Allen & Fairchild 5191*. COCLÉ: vic. El Valle de Antón, 800–1000 m., *Allen 780*. CHIRIQUÍ: upper Río Chiriquí Viejo, 1300–1900 m., *White & White 37*; vic. Finca Lérida, eastern slopes of Chiriquí Volcano, 5000 ft., *R. K. Morris s. n.*; vic. Bajo Mono and Quebrada Chiquero, 1500 m., *Woodson & Schery 563*; Bajo Mono-Robalo trail, western slopes of Cerro Horqueta, 5000–7000 ft., *Allen 4783*.

A common species of very variable vegetative habit, widely distributed throughout our area.

28. MAXILLARIA OREOCHARIS Schltr. in Fedde Rep. Sp. Nov. Beih. 17:69. 1922.

Erect or pendulous, epiphytic herbs. Pseudobulbs strongly ancipitous, oblong-elliptic, monophyllous, 3–4 cm. long and 1.0–1.5 cm. wide, approximate and often more or less imbricating, obliquely inserted on the rhizome, the bases provided with several imbricating bracts, the upper 1–3 of which are conspicuously long-foliaceous, the short internodes enveloped in closely imbricating, more or less complanate, persistent, acute, papery bracts. Leaves subcoriaceous, linear, acute or acuminate, 25–40 cm. long and .6–1.0 cm. wide, contracted below into very short, conduplicate petioles. Inflorescences usually solitary, slender, 1-flowered scapes 3–4 cm. long, produced from the base of the mature pseudobulbs. Sepals subequal, free, more or less spreading, lanceolate, acute, white with red markings,

about 1.5 cm. long and .3–.4 cm. wide, the laterals adnate to the column foot, forming an inconspicuous, subacute mentum. Petals subequal to the dorsal sepal, lanceolate, acute, white, about 12 mm. long and 2.5–3 mm. wide. Lip oblong-ligular, acute, 3-lobed near the apex, about 12 mm. long and 5 mm. wide when spread out, the base articulated with the foot of the column, the lateral lobes erect in natural position, dark red, the mid-lobe ovate, subacute, somewhat thickened, about ⅓ the total length of the lip, yellow, the upper surface and margins minutely papillose-puberulent; the disk with a linear, obtuse, fleshy callus, about ¾ the length of the lateral lobes. Column slender, semi-terete, somewhat arcuate, the apex dilated, about 7 mm. long, white, the base produced into a foot.

Costa Rica and Panama.

CHIRIQUÍ: without definite locality, 4000–5000 ft., *Powell 256.*

29. MAXILLARIA PARVILABIA Ames & Schweinf. in Sched. Orch. 8:62. 1925.

Erect, epiphytic herbs without pseudobulbs; the woody, often branching, cylindric canes 1–1.25 m. tall, the lower portions closely enveloped in the persistent leaf bases, the apices with 2-ranked foliage. Leaves coriaceous, linear-lanceolate, obtuse or retuse and obliquely 2-lobed at the apex, 4–15 cm. long and .6–1.2 cm. wide, the tubular, clasping bases closely imbricating and equidistantly distributed on the stems. Inflorescences few to many slender, 1-flowered scapes about 4 cm. long, produced singly or in loose fascicles from the leaf axils. Flowers pale yellow, of moderate size. Sepals subequal, free, spreading, lanceolate, acute, 1.6–2 cm. long and .4–.5 cm. wide, the laterals adnate to the foot of the column, forming a short, subacute mentum. Petals subequal to the dorsal sepal, elliptic-lanceolate, acute, 1.3–1.5 cm. long and .4–.5 cm. wide. Lip small, obscurely 3-lobed, elliptic-obovate, 5–6 mm. long and 3–3.5 mm. wide when spread out, contracted at the base and articulated with the foot of the column, the lateral margins somewhat erect in natural position, distinct only at the small acute apices, mid-lobe fleshy, ovate, acute, about ⅖ the total length of the lip, the apex lightly recurved; the disk with a small fleshy linguiform callus, about ½ the length of the lateral lobes. Column short, stout, semi-terete, about 2.5 mm. long, produced at the base into a short foot.

Costa Rica and Panama.

CHIRIQUÍ: vic. Bajo Chorro, in rain forest, headwaters of the Río Caldera, 6000 ft., *Davidson 126.*

30. MAXILLARIA PITTIERI (Ames) L. Wms. in Ann. Mo. Bot. Gard. 29:349. 1942.

Ornithidium Pittieri Ames, in Sched. Orch. 2:35. 1923.

Erect or pendulous, epiphytic herbs with woody, branching, cylindric canes up to about 1.5 m. tall, the lower portions naked or enveloped in the persistent, tubular leaf bases, the apex with sparse clusters of 2-ranked foliage, portions of which may persist at distant intervals along the stems. Leaves coriaceous, ligular, acute, 7–15 cm. long and 1–2 cm. wide, the conduplicate bases forming a sheathing

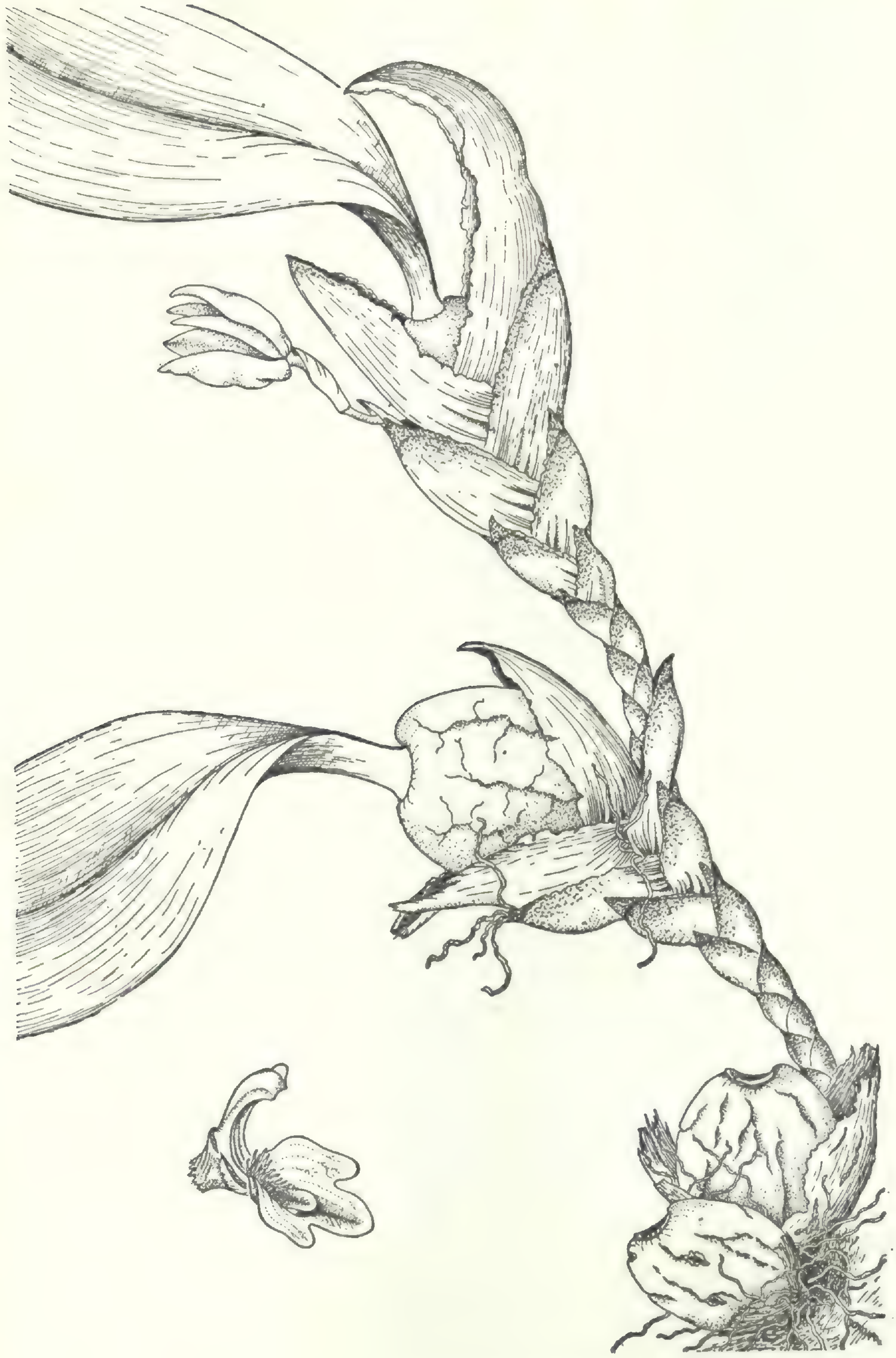


Fig. 184. *Maxillaria planicola*

petiole. Inflorescences short 1-flowered scapes, produced in dense fascicles from the axils of the leaves. Flowers small, pink. Sepals free, subequal, not spreading, concave, ovate, acute, with a central keel, 8–9 mm. long and about 4 mm. wide, the laterals adnate to the somewhat produced base of the column, forming a short, rounded mentum. Petals subequal to the dorsal sepal, concave, oblong-ovate, acute, 7 mm. long and about 3 mm. wide. Lip fleshy, entire, about 4 mm. long and 2.5 mm. wide, the base deeply concave and adnate to the base of the column, the apex lanceolate, obtuse to subacute, conspicuously thickened. Column short, stout, about 2.5 mm. long, the base with conspicuous lateral thickenings.

Costa Rica and Panama.

CHIRIQUÍ: Bajo Chorro, in rain forest, headwaters of the Río Caldera, 6000 ft., *Davidson 117*.

31. MAXILLARIA PLANICOLA C. Schweinf. in Bot. Mus. Leafl. Harv. Univ. 8:188. 1940.

Camaridium latifolium Schltr. in Fedde, Rep. Sp. Nov. Beih. 17:74. 1922, non *Maxillaria latifolia* Lindl.

Epiphytic herbs with elliptic-ovate to elliptic-oblong, compressed, monophyllous pseudobulbs 3.5–6 cm. long and 1.5–4 cm. wide, the internodes of the mature plants 6–8 cm. long and 8–12 mm. thick, enveloped in closely imbricating, tubular, acute, papery bracts, the upper 3–6 of which are complanate-spathaceous, the conduplicate bases covering the lower half of the pseudobulb. Leaves coriaceous, ligular to elliptic-lanceolate, acute, 15–35 cm. long and 3–6 cm. wide, contracted below into narrow, conduplicate petioles. Inflorescences usually 2–4 slender 1-flowered scapes, 4–5 cm. long, produced from the axils of the spathaceous, sheathing bracts after the current pseudobulb has nearly matured. Flowers relatively large and conspicuous. Sepals subequal, free, not spreading, concave, the dorsal sepal lanceolate, acute, 3–3.5 cm. long and .8–1.0 cm. wide, the laterals elliptic-lanceolate, acute, 3–3.5 cm. long and 1.0–1.2 cm. wide, adnate to the foot of the column, forming an inconspicuous, rounded mentum. Petals white, lanceolate, acute, 2.8–3.2 cm. long and .6–.7 cm. wide. Lip conspicuously 3-lobed, white, 18–20 mm. long and 18–20 mm. wide when spread out, contracted at the base and articulated with the foot of the column, the lateral lobes erect and incurving over the column in natural position, the acute apices projecting, the mid-lobe triangular, acute, about ⅓ the total length of the lip; the disk with a short, fleshy, ligular, obtuse callus about ¾ the length of the lateral lobes, the basal half yellow, densely and conspicuously pilose. Column semi-terete, somewhat arcuate, 10–12 mm. long, produced at the base into a short foot.

Panama.

CANAL ZONE: vic. San Juan de Pequení, upper Madden Lake region, *Powell 3438*; vic. Vigía and San Juan de Pequení, 66 m., *Dodge, Steyermark & Allen 16580*. PANAMÁ: hills east of Panama City, *Powell 8*; Cerro Campana, vic. Campana, on sheer rock face, 2500 ft., *Allen 5078*. COLÓN: vic. Porto Bello, sea level, *Powell 3458*.

32. MAXILLARIA POWELLII Schltr. in Fedde Rep. Sp. Nov. Beih. 17:70. 1922.

Erect, epiphytic herbs with approximate, fleshy, ovoid to elliptic-ovoid, compressed, monophyllous pseudobulbs 2–4 cm. long and 1.5–2 cm. wide, the bases enveloped in several papery, imbricating bracts which often weather away to loose fibers. Leaves coriaceous, ligular, obtuse to subacute, 15–40 cm. long and 2–3 cm. wide, contracted below into slender, conduplicate petioles. Inflorescences usually 2–4 slender, 1-flowered scapes 4–6 cm. long, produced from the bases of the pseudobulbs. Flowers of moderate size. Sepals subequal, free, spreading, yellow or tan, the dorsal sepal concave, 1.5–1.8 cm. long and .4–.6 cm. wide, ligular to elliptic-lanceolate, obtuse, with a minute apicule, the laterals ligular to elliptic-lanceolate, obtuse, 1.8–2 cm. long and .4–.8 cm. wide, the oblique bases adnate to the foot of the column forming a short, subacute mentum. Petals subequal to the dorsal sepal, yellow or tan, rather obliquely ligular, acute, 1.5–1.7 cm. long and .4–.5 cm. wide. Lip conspicuously 3-lobed near the apex, 1.4–1.6 cm. long and .7–.8 cm. wide when spread out, contracted at the base and articulated with the foot of the column, the lateral lobes yellow or tan, erect in natural position, the acute to obtuse apices projecting, the mid-lobe ovate, acute, fleshy, rugulose, minutely pilose, usually reddish brown, about ⅓ the total length of the lip, the under-surface of the apex with a triangular keel; the disk with a low, ligular callus about ¾ the length of the lateral lobes. Column semi-terete, somewhat arcuate, 7–8 mm. long, produced at the base into a foot. Anther terminal, operculate, incumbent, 1-celled.

Panama.

CANAL ZONE: vic. Frijoles, Gatún Lake, sea level, *Powell 28*. PANAMÁ: Cerro Campana, 2400 ft., *Allen & Fairchild 3973, 4235, 4237*. COCLÉ: vic. El Valle de Antón, 600 m., *Allen 2073;* mossy forest on the crest of Cerro Pajita, hills north of El Valle, 1200 m., *Allen 4254*.

A common small-flowered species, rather doubtfully distinct from *Maxillaria ringens*.

33. MAXILLARIA REPENS L. Wms. in Amer. Orch. Soc. Bull. 10:273, *t. 9*. 1942.

Repent, epiphytic herbs with elongate, slender, often branching stems enveloped in tubular, papery sheaths which often weather away, the caespitose 2-ranked foliaceous growths usually freely rooting from the base, distant or terminal on the stems. Leaves 3–5, coriaceous, 3–10 cm. long and 1–2 cm. wide, elliptic-lanceolate, acute, the conduplicate bases closely imbricating, forming a complanate, sheathing petiole. Inflorescences usually several slender, 1-flowered scapes 1.5–2 cm. long, produced from the axils of the leaves. Flowers small. Sepals subequal, green with reddish brown margins, lanceolate, acute, 7–10 mm. long and 2.5–3.5 mm. wide, the dorsal sepal concave and incurving over the column, the laterals adnate to the foot of the column, widely spreading or reflexed. Petals subequal to and parallel with the dorsal sepal, green with reddish brown margins, linear-lanceolate, acute, 6.5–7.5 mm. long and 2–3 mm. wide. Lip conspicuously 3-

Fig. 185. *Maxillaria repens*

lobed, 6–8 mm. long and 3.5–4.5 mm. wide, the basal half canaliculate and adnate to the foot of the column, the lateral lobes erect and parallel with the column, the area between the truncate apices with a short, obtuse, concave, fleshy callus; the mid-lobe broadly spreading, subquadrate, strongly reflexed, the truncate apex deeply emarginate, the center orange-yellow with pale yellow, undulate margins, the under-surface with a short, fleshy, apiculate keel. Column stout, semi-terete, about 5 mm. long, produced at the base into a short, stout foot.

Panama.

COCLÉ: region north of El Valle de Antón, trail to Las Minas, 1000 m., *Allen 2868;* mossy forest on the crest of Cerro Pajita, hills north of El Valle, 1200 m., *Allen & Fairchild 3946, Allen & Allen 3792.*

34. MAXILLARIA RINGENS Rchb. f. in Walp. Ann. 6:523. 1863.

Maxillaria Tuerckheimii Schltr. in Fedde Rep. Sp. Nov. 10:295. 1912.
Maxillaria Rousseauae Schltr. in Beih. Bot. Centralbl. 36^2:413. 1918.
Maxillaria pubilabia Schltr. in Fedde Rep. Sp. Nov. Beih. 17:71. 1922.
Maxillaria Amparoana Schltr. loc. cit. 19:54. 1923.
Maxillaria Brenesii Schltr. loc. cit. 231. 1923.
Maxillaria lactea Schltr. loc. cit. 233. 1923.

Erect, epiphytic herbs with fleshy, approximate, elliptic-ovoid, compressed, monophyllous pseudobulbs 2.5–5.5 cm. long and 2–3 cm. wide, the bases enveloped in several papery, imbricating bracts which become more or less fibrous with age. Leaves coriaceous, ligular, obtuse to acute, 15–40 cm. long and 2–4.5 cm. wide, contracted below into short or elongate, conduplicate petioles. Inflorescences 1 to about 6 slender, 1-flowered scapes 5–12 cm. long, produced singly or in loose fascicles from the bases of the pseudobulbs. Flowers relatively large. Sepals free, subequal, spreading, yellow, white, or tan, sometimes shaded pink or lavender, ligular, obtuse to lanceolate, acuminate, 2.5–4 cm. long and .3–.6 cm. wide, the laterals adnate to the column foot, forming a short, rounded or subacute mentum. Petals subequal to the dorsal sepal, white or pale yellow, lanceolate, acute to acuminate, 2.2–3.5 cm. long and .25–.4 cm. wide. Lip 3-lobed near the apex, 10–15 mm. long and 6–8 mm. wide when spread out, white marked with lavender to yellow marked maroon, contracted at the base and articulated with the column foot, the lateral lobes erect, the obtuse to acute apices projecting, the mid-lobe rhombic-ovate to obovate, obtuse to acute, fleshy and more or less rugose or minutely papillose on the upper surface, about ⅓ the total length of the lip, the under-surface of the apex transversely thickened or with an acute central keel; the disk with a ligular callus about ¾ the length of the lateral lobes. Column semi-terete, somewhat arcuate, about equaling the lateral lobes of the lip, the base produced into a short foot.

Mexico, British Honduras, Guatemala, Honduras, Nicaragua, Costa Rica, Panama to Peru.

COCLÉ: region north of El Valle de Antón, 800–1000 m., *Allen 2264, 2871, 2873;*

mountains beyond La Pintada, 400–600 m., *Hunter & Allen 560.* CHIRIQUÍ: without definite locality, 4000 ft., *Powell 3443, 3466.*

A common, very variable species, widely distributed throughout the intermediate highlands of central and northern South America.

35. MAXILLARIA RUFESCENS Lindl. in Bot. Reg. 21: sub *t. 1802.* 1836.

Maxillaria Abelei Schltr. in Fedde Rep. Sp. Nov. Beih. 9:101. 1921.

Erect, epiphytic herbs with approximate, ovoid-elliptic to linear, compressed, fleshy, monophyllous pseudobulbs 2.5–4.5 cm. long and 6–22 mm. wide, the bases enveloped in several papery, imbricating bracts which become fibrous with age. Leaves coriaceous, ligular, acute or rarely acuminate, 15–32 cm. long and 1.2–3.5 cm. wide, contracted below into short or elongate, conduplicate petioles. Inflorescences slender, usually solitary, 1-flowered scapes 3.5–4 cm. long, produced from the bases of the pseudobulbs. Flowers of moderate size. Sepals subequal, free, spreading, creamy white or yellow, elliptic-oblong, obtuse to subacute, 1.4–2 cm. long and .5–.7 cm. wide, the laterals adnate to the foot of the column, forming a short, rounded mentum. Petals subequal to the dorsal sepal, white or yellow, elliptic-lanceolate, obtuse to shortly acute, 12–15 mm. long and 5–7 mm. wide. Lip conspicuously 3-lobed, orange to yellow with reddish brown or purple markings, 10–12 mm. long and 5–6 mm. wide when spread out, the base contracted and articulated with the column foot, the lateral lobes erect in natural position, the acute apices conspicuously projecting, the mid-lobe broadly oblong, about $\frac{3}{5}$ the total length of the lip, the truncate apex usually emarginate; the disk with a fleshy, ligular callus equaling or exceeding the lateral lobes in length. Column stout, somewhat arcuate, semi-terete, 10–12 mm. long, the base produced into a short foot.

Guatemala, Honduras, Nicaragua, Costa Rica, Panama, British Guiana, Peru, Brazil, Cuba, Hispaniola, Jamaica, Trinidad, and probably other adjacent areas.

COCLÉ: mountains beyond La Pintada, 400–600 m., *Hunter & Allen 563*; vic. El Valle de Antón, 600–1000 m., *Allen 1255.*

36. MAXILLARIA UMBRATILIS L. Wms. in Ann. Mo. Bot. Gard. 28:425. 1941.

Camaridium nutantiflorum Schltr. in Beih. Bot. Centralbl. 36^2:417. 1918, non *Maxillaria nutantiflora* Schltr.

Erect or pendulous, epiphytic herbs with elongate, sometimes branching stems. Pseudobulbs elliptic-ovoid, ancipitous, monophyllous, 2.5–4 cm. long and 1.5–2 cm. wide, very distantly and obliquely inserted on the canes, the lower half covered by the conduplicate bases of the 3–5 long-foliaceous bracts; the long internodes naked or enveloped in the persistent bases of the imbricating bracts. Leaves of the apex of the pseudobulb and those of the basal long-foliaceous bracts subcoriaceous, ligular, acute or obtuse, 8–30 cm. long and 1.2–2.2 cm. wide. Inflorescences slender, 1-flowered scapes 3–5 cm. long, produced from the bract axils of the elongate, complanate flush of new growth. Flowers of moderate size. Sepals

free, subequal, spreading, yellowish green, lanceolate, acute, 2–2.5 cm. long and 4–6 mm. wide, the laterals adnate to the foot of the column, forming a short, rounded mentum. Petals subequal to the dorsal sepal and similarly colored, obliquely lanceolate, acute to acuminate, 15–18 mm. long and 3.5–5 mm. wide. Lip conspicuously 3-lobed, red or marked with red, 10–12 mm. long and 10–12 mm. wide when spread out, the base contracted and articulated with the foot of the column, the lateral lobes subfalcate, acute, erect in natural position and somewhat incurving over the column, the apices projecting, the mid-lobe ovate, acute, about ½ the total length of the lip; disk with a short, broad, truncate, fleshy callus about ⅓ the length of the lateral lobes. Column very short, stout, about 5 mm. long, produced at the base into a short foot.

Costa Rica and Panama.

CHIRIQUÍ: vic. Bajo Chorro, headwaters of the Río Caldera, in rain forest, 6000 ft., *Davidson 308*.

37. MAXILLARIA UNCATA Lindl. in Bot. Reg. 23: sub *t. 1986*. 1837.

Maxillaria Macleei Batem. ex Lindl. in Bot. Reg. 26: Misc. 70. 1840.
Maxillaria stenostele Schltr. in Beih. Bot. Centralbl. 36^2:414. 1918.

Slender, erect or pendulous, epiphytic herbs with short to elongate, often branching stems 4–40 cm. long. Pseudobulbs minute, linear-complanate to terete, monophyllous, 4–10 mm. long and 2–3.5 mm. wide, approximate to rather remote, obliquely inserted on the stems, pseudobulbs and internodes enveloped in broad, brown, imbricating, scarious sheaths. Leaves fleshy, subulate-conduplicate, semiterete or rarely lanceolate-elliptic, acute to acuminate, 2–6 cm. long and .2–1.0 cm. wide. Inflorescences short, usually solitary, 1-flowered scapes 10–20 mm. long, produced from the base of the current mature growth. Flowers small, translucent with red or purple stripes. Sepals free, not spreading, the dorsal sepal oblong, obtuse to acute, concave, 7–9 mm. long and about 3 mm. wide, the laterals lanceolate, acute, 10–12 mm. long and 3–4 mm. wide, the very long, oblique bases adnate to the foot of the column, forming an elongate, conspicuous, obtuse to subacute mentum. Petals ligular to oblanceolate, acute, about equaling the dorsal sepal in length. Lip linear-oblanceolate, obtuse to subacute, entire, somewhat exceeding the lateral sepals, 12–14 mm. long and 3–3.5 mm. wide at the apex, the long narrow base slightly concave and articulated with the foot of the column, the subrotund to subacute apex often with undulate margins; the disk with a linear, obtuse callus about ½ the total length of the lip. Column elongate, semiterete, somewhat arcuate, the apex with short, lateral, subfalcate, deflexed wings; the base produced into an elongate foot.

British Honduras, Guatemala, Honduras, Costa Rica, Panama, Peru, British Guiana, Brazil, and probably adjacent areas.

CANAL ZONE: Río Pequení, upper Madden Lake region, 66–70 m., *Dodge, Steyermark & Allen 16752*. PANAMÁ: hills east of Panama City, sea level to about 200 ft., *Powell 120*. COLÓN: Quebrada López, lower forested slopes of Cerro Santa Rita, about 30 m., *Allen 2141*. COCLÉ: hills north of El Valle de Antón, 600–1000 m., *Allen 1682, 3715*. BOCAS DEL TORO: without definite locality, *von Wedel 489*.

38. MAXILLARIA VAGANS Ames & Schweinf. in Sched. Orch. 8:65. 1925.

Erect or pendulous, epiphytic herbs with stout, simple or branching stems 15–45 cm. long, the lower portions usually conspicuously enveloped in numerous fibrous roots. Pseudobulbs fleshy, monophyllous, elliptic-oblong, compressed and rugose, 1.5–3 cm. long and 1.0–1.5 cm. wide, approximate or distant, inserted at an acute angle on the stems, the current pseudobulb partly covered by the conduplicate bases of several long-foliaceous bracts, the internodes and old pseudobulbs entirely invested by the persistent bract bases. Leaves of the apex of the pseudobulbs and the blades of the foliaceous bracts coriaceous, ligular, obtuse, or the apex retuse and unequally bilobed, 4.5–18 cm. long and 1–2.5 cm. wide. Inflorescences slender, 1-flowered scapes 3–4 cm. long, usually produced from the base of the current mature pseudobulb but sometimes from the axils of the flush of new growth. Flowers of moderate size. Sepals free, spreading, red or pink with yellow or green margins, the dorsal sepal linear-lanceolate to elliptic-lanceolate, acute, arching over the column, 1.7–2.3 cm. long and .5–.7 cm. wide, the dorsal surface with a keel which terminates in an apicule, the lateral sepals spreading, elliptic-lanceolate, acute, 1.8–2.2 cm. long and .5–.7 cm. wide, adnate at the base to the column foot, forming a short, rounded mentum. Petals ligular to oblanceolate, acute, similarly colored with the sepals, 1.5–2 cm. long and .5–.6 cm. wide. Lip conspicuously 3-lobed, red margined white, or yellow with the apical lobe spotted rose-pink, 12–16 mm. long and 6–8 mm. wide, contracted at the base and articulated with the foot of the column, the lateral lobes rounded, erect in natural position, the mid-lobe fleshy, obovate, acute, canaliculate, with ascending margins, more than half the total length of the lip, the lower surface with a strongly developed keel; disk with a short, fleshy, emarginate callus. Column semi-terete, somewhat arcuate, 6–8 mm. long, produced at the base into a short foot. Anther terminal, operculate, incumbent, 1-celled.

Costa Rica and Panama.

COCLÉ: mountains beyond La Pintada, 400–600 m., *Hunter & Allen 598;* region north of El Valle de Antón, trail to Las Minas, 1000 m., *Allen 2893;* mossy forest on crest of Cerro Pajita, hills north of El Valle, 1000 m., *Allen 4177.* CHIRIQUÍ: Palo Alto, 4500–5000 ft., *Powell 348.*

A fairly frequent highland species closely allied to *Maxillaria cucullata.*

39. MAXILLARIA VALENZUELANA (A. Rich.) Nash, in Bull. Torr. Bot. Club. 34:121. 1907.

Dicrypta iridifolia Batem. in Loud. Hort. Brit. Suppl. 2:630. 1839, nomen nudum.
Pleurothallis valenzuelana A. Rich. in Sagra, Hist. Isla Cuba 11 [Fl. Cub. Fanerog.]:234. 1850.
Maxillaria iridifolia (Batem.) Rchb. f. in Bonplandia 2:16. 1854.
Dicrypta irisphyta Barb. Rodr. Gen. & Spec. Orch. 1:126. 1877.

Pendulous epiphytic herbs without pseudobulbs. Leaves distichously arranged in the form of a broad fan, rather fleshy, gladiate, lanceolate, acuminate, 9–30 cm. long and 1.0–2.5 cm. wide, the broad conduplicate bases closely imbricating. In-

florescences short, 1-flowered scapes, solitary or in dense fascicles in the axils of the leaves. Flowers of moderate size. Sepals free, subequal, spreading, yellow, elliptic-lanceolate, acute, 10–12 mm. long and 4–6 mm. wide, the laterals somewhat oblique, the bases adnate to the column foot, forming an inconspicuous, rounded mentum. Petals lanceolate, acute, yellow, 8–10 mm. long and 2.5–3.5 mm. wide. Lip entire or obscurely 3-lobed, yellow with purple or maroon markings, elliptic-ovate, acute, 9–11 mm. long and 4–5 mm. wide when spread out, the base contracted and articulated with the column foot, the lateral margins erect in natural position, the mid-lobe thickened at the apex and on the margins, about ½ the total length of the lip; disk with a ligular callus running the full length of the lip, somewhat thickened near the apices of lateral margins. Column short, stout, somewhat arcuate, produced at the base into a short foot.

Cuba, Honduras, Costa Rica, Panama, Colombia, Venezuela, Brazil, and probably adjacent areas.

CHIRIQUÍ: vic. Boquete, 3800 ft., *Davidson 636.*

A frequent, pendulous, fan-leaved epiphyte of the Chiriquí highlands.

40. MAXILLARIA VARIABILIS Batem. ex Lindl. in Bot. Reg. 23: sub *t. 1986.* 1837.

Maxillaria Henchmanni Hook. in Bot. Mag. *t. 3614.* 1837.
Maxillaria angustifolia Hook. Ic. Plant. 4: *t. 348.* 1841.
Maxillaria Lyonii Lindl. in Bot. Reg. n. s. 8: Misc. 17. 1845.
Maxillaria revoluta Kl. in Allgem. Gartenzeit. 20:186. 1852.
Maxillaria chiriquensis Schltr. in Fedde Rep. Sp. Nov. Beih. 17:68. 1922.
Maxillaria panamensis Schltr. loc. cit. 70. 1922.
Maxillaria costaricensis Schltr. loc. cit. 19:232. 1923.

Erect or pendulous, epiphytic herbs with short or elongate, usually simple stems of very variable vegetative appearance, 5–30 cm. long. Pseudobulbs linear to elliptic-oblong, subcylindric to strongly ancipitous, usually rugose, 1.5–6 cm. long and .3–2.0 cm. wide, approximate and inserted at an acute angle on the stems, the truncate apices monophyllous, the internodes and bases enveloped in closely imbricating, papery bracts. Leaves coriaceous, ligular, obtuse or 2-lobed at the apex, 3–15 cm. long and .3–1.6 cm. wide, contracted below into very short, conduplicate petioles. Inflorescences slender, 1-flowered, often solitary scapes produced from the bract axils of the flush of new growth, or sometimes from the base of the current mature pseudobulb. Flowers usually of moderate size or small, white or yellow marked with dark red, or with a red lip, or entirely dark red. Sepals subequal, free, more or less spreading, linear-lanceolate to elliptic-lanceolate, obtuse, with a minute apicule or sometimes acute, 6–12 mm. long and 2–4 mm. wide, the laterals adnate to the foot of the column, forming a short, subacute mentum. Petals lanceolate to oblanceolate, acute, 5–10 mm. long and 1.5–3.5 mm. wide. Lip entire or obscurely 3-lobed near the apex, 6–12 mm. long and 3–6 mm. wide when spread out, the base articulated with the column foot, the lateral margins rounded and erect in natural position, the mid-lobe subacute to truncate and

shallowly emarginate, about ⅓ the total length of the lip; the disk with a ligular, obtuse callus nearly equalling the lateral lobes. Anther terminal, operculate, incumbent, 1-celled.

Mexico, British Honduras, Guatemala, Salvador, Honduras, Nicaragua, Costa Rica, Panama, British Guiana, and probably adjacent territories.

PANAMÁ: hills near Panama City, sea level, *Powell 124.* COCLÉ: vic. El Valle de Antón, 600–1000 m., *Allen 1252, 3716, 3813.* CHIRIQUÍ: without definite locality, 4000 ft., *Powell 125;* vic. Boquete, 4000–4500 ft., *Powell 418;* Cerro de Lino, vic. Boquete, 1000–1300 m., *Pittier 3017;* vic. Boquete, 3800 ft., *Davidson 645;* vic. Monte Lirio, upper Río Chiriquí Viejo, *G. White 38;* vic. New Switzerland, Río Chiriquí Viejo, 1800–2000 m., *Allen 1339.*

41. MAXILLARIA WERCKLEI (Schltr.) L. Wms. in Ann. Mo. Bot. Gard. 27:284. 1940.

Ornithidium Wercklei Schltr. in Fedde Rep. Sp. Nov. Beih. 19:60. 1923.
Maxillaria aurantiaca Schltr. loc. cit. 27:87. 1924.
Maxillaria Lankesteri Ames, in Sched. Orch. 7:11. 1924.

Erect or pendulous, epiphytic herbs with slender, branching stems 3–20 cm. tall. Pseudobulbs linear, compressed, rugose in dried specimens, 4–25 mm. long and 1.5–5 mm. wide, distantly inserted on the stems, the truncate apices monophyllous, the bases with 2–3 conspicuous, long-foliaceous bracts, the long internodes enveloped in persistent, closely imbricating, complanate sheaths. Leaves of the apex of the pseudobulbs and the blades of the foliaceous bracts coriaceous, ligular to elliptic-lanceolate, broadly obtuse, or retuse at the apex, 1–3 cm. long and .2–1.2 cm. wide, contracted below into very short, subsessile, conduplicate petioles. Inflorescences slender, 1-flowered scapes 4–10 mm. long, produced from the bract axils of the flush of new growth. Flowers very variable, small or of moderate size, usually tan striped red or brown to dark reddish purple. Sepals subequal, free, spreading, lanceolate to elliptic-lanceolate, acute, 5–12 mm. long and 2.5–5 mm. wide, the apices sometimes carinate, the laterals adnate to the foot of the column, forming a short, rounded mentum. Petals subequal to the dorsal sepal, oblong-lanceolate, obtuse to subacute, 4–11 mm. long and 2–4 mm. wide. Lip 3-lobed near the base, 4–10 mm. long and 3–6 mm. wide, contracted at the base and articulated with the column foot, the short, lateral lobes rounded or subacute, obliquely erect in natural position, separated near the apices by a transverse, fleshy callus, mid-lobe elliptic-ovate to oblong, convex, the margins often deflexed or revolute, the apex obtuse to subacute, ⅗ to ¾ the total length of the lip. Column short, stout, semi-terete, somewhat arcuate, produced at the base into a distinct foot. Anther terminal, operculate, incumbent, 1-celled.

Costa Rica, Panama, and Colombia.

COCLÉ: hills north of El Valle de Antón, 1000 m., *Allen 1253.*

(To be concluded in Part III, Fasc. 5)

STAFF
OF THE MISSOURI BOTANICAL GARDEN

Director
GEORGE T. MOORE

HERMANN VON SCHRENK,
Pathologist

ROBERT W. SCHERY,
Research Associate

JESSE M. GREENMAN,
Curator Emeritus of the Herbarium

GUSTAV A. L. MEHLQUIST,
Research Horticulturist

CARROLL W. DODGE,
Mycologist

ROLLA M. TRYON,
Assistant Curator of the Herbarium

EDGAR ANDERSON,
Geneticist

GEORGE B. VAN SCHAACK,
Honorary Curator of Grasses

ROBERT E. WOODSON, JR.
Curator of the Herbarium

JULIAN A. STEYERMARK,
Honorary Research Associate

HENRY N. ANDREWS,
Paleobotanist

NELL C. HORNER,
Librarian and Editor of Publications

GERALD ULRICI,
Business Manager

BOARD OF TRUSTEES
OF THE MISSOURI BOTANICAL GARDEN

President
RICHARD J. LOCKWOOD

Vice-President
DANIEL K. CATLIN

Second Vice-President
EUGENE PETTUS

L. RAY CARTER
DUDLEY FRENCH
HENRY HITCHCOCK
JOHN S. LEHMANN
GEORGE T. MOORE
A. WESSEL SHAPLEIGH
ETHAN A. H. SHEPLEY

EX-OFFICIO MEMBERS

ARTHUR H. COMPTON,
Chancellor of Washington University

WILLIAM P. GRUNER,
President of the Academy of Science of St. Louis

A. P. KAUFMANN,
Mayor of the City of St. Louis

WILLIAM SCARLETT,
Bishop of the Diocese of Missouri

C. OSCAR JOHNSON
President of the Board of Education of St. Louis

GERALD ULRICI, *Secretary*

Volume XXXVI Number 2

Annals
of the
Missouri Botanical
Garden

MAY, 1949

Flora of Panama. Part III. Fascicle 5 (Orchidaceae, fourth part) . .
. Robert E. Woodson, Jr., Robert W Schery and Collaborators 133–245

PUBLISHED QUARTERLY AT GALESBURG, ILLINOIS,
BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN,
ST. LOUIS, MISSOURI.

Entered as second-class matter at the post office at Galesburg, Illinois,
under the Act of March 3, 1879.

Annals
of the
Missouri Botanical Garden

A Quarterly Journal containing Scientific Contributions from the Missouri Botanical Garden and the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

Information

The ANNALS OF THE MISSOURI BOTANICAL GARDEN appears four times during the calendar year: February, May, September, and November. Four numbers constitute a volume.

Subscription Price _____ $10.00 per volume
Single Numbers _____ 2.50 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

FLORA OF PANAMA

Part III. Fascicle 4

ORCHIDACEAE

By PAUL H. ALLEN

66. TRIGONIDIUM Lindl.

TRIGONIDIUM Lindl. in Bot. Reg. 23: *t. 1923*. 1837; Benth. & Hook. Gen. Pl. 3:567. 1883.

Caespitose, erect, repent, or scandent epiphytic herbs with short ovoid or elliptic-ovoid, compressed, usually ridged and sulcate pseudobulbs, the apices with 1–5 linear to elliptic-lanceolate, coriaceous or subcoriaceous leaves. Inflorescences simple, slender, short or elongate, 1-flowered scapes produced from the bases of the pseudobulbs. Flowers relatively large. Sepals subequal, the bases connivent, forming a tube, the apical portions spreading or reflexed. Petals much smaller than the sepals. Lip distinctly 3-lobed, very small, shorter than the petals, the lateral lobes erect and paralleling the column, the mid-lobe spreading, often thickened or tuberculate, the apex usually recurved; disk with a fleshy, usually ligular callus. Column short, rather stout, semiterete, wingless, the base without a foot. Anther terminal, operculate, incumbent, 1-celled; pollinia 4, waxy.

A small genus of tropical American epiphytes, ranging from Mexico to Brazil. Two species are known from Panama.

a. Pseudobulbs approximate, the apex with 2 leaves. Petals not apiculate. Lowland species ..... 1. T. EGERTONIANUM
aa. Pseudobulbs widely separated on a cylindric rhizome, the apex with 3–5 leaves. Petals conspicuously apiculate. Highland species ..... 2. T. LANKESTERI

1. TRIGONIDIUM EGERTONIANUM Batem. ex Lindl. in Bot. Reg. n. s. 1: Misc. 73. 1838.

Trigonidium Seemanni Rchb. f. in Seem. Bot. Voy. Herald, p. 214. 1854.

Erect epiphytic herbs with approximate, ovoid to elliptic-ovoid, ridged and sulcate, diphyllous pseudobulbs 3.5–7 cm. long and 1.5–4 cm. wide, the bases enveloped in 3–5 brown, imbricating bracts which become fibrous with age. Leaves subcoriaceous, linear-lanceolate, acute, 20–60 cm. long and .8–3 cm. wide, contracted below into slender, conduplicate petioles. Inflorescences 1 to several

Issued June 18, 1949.

Fig. 186. *Trigonidium Egertonianum*

slender, erect, 1-flowered scapes, 20–40 cm. long, produced from the bases of the pseudobulbs, enveloped throughout in tubular, papery, imbricating bracts. Flowers relatively large. Sepals free, the bases connivent, forming a tube, usually greenish yellow to pinkish tan, with brown or purple stripes; the dorsal sepal elliptic-oblanceolate, acute, spreading, 2.5–4.5 cm. long and 1–2 cm. wide, the laterals obliquely oblong to elliptic-lanceolate, acute, the apices strongly recurved, 27–42 mm. long and 8–14 mm. wide. Petals lanceolate to oblanceolate, acute, greenish yellow to pinkish tan, striped brown or purple, 12–22 mm. long and 4–6 mm. wide, with a brown to purple gland-like thickening near the apex. Lip 3-lobed, about ⅓ the length of the petals, yellowish tan striped brown or red, 5–6 mm. long and 3–4 mm. wide when spread out, contracted at the base and articulated with the base of the column, the lateral lobes erect and paralleling the column, the mid-lobe ovate, acute, pale yellow with a darker center, rather fleshy, ⅓ to ⅖ the total length of the lip, the apex recurved and verrucose on both the upper and lower surfaces, the disk with a fleshy ligular callus about equaling the lateral lobes in length. Column semiterete, purple, 4–5 mm. long, the base footless.

Mexico, British Honduras, Guatemala, Salvador, Honduras, Nicaragua, Costa Rica, Panama, and Colombia.

CANAL ZONE: vicinity Frijoles, sea level, *Powell 3023;* drowned forest of the upper Río Pequení, Madden Lake region, 70 m., *Allen 17281;* forest along banks above Río Indio Hydrographic Station, Madden Lake region, 70–75 m., *Steyermark 17426;* vicinity Gamboa, 20–100 m., *Pittier 2613;* Barro Colorado Island, Gatún Lake, *Zetek s. n., Woodworth & Vestal 593.* PANAMÁ: along road to Pacora, about 50 m., *Allen 820;* hills east of Panama City, *Powell 44.* COLÓN: Cerro Santa Rita, 1200 ft., *Allen & Fairchild 5194;* Río Gatuncillo, vicinity Santa Rosa, 100 ft., *Allen & Allen 4159.* VERAGUAS: Bahia Honda, *Taylor 1515; Elmore H-48;* vicinity Soná, about 100 ft., *Allen & Allen 4240.* BOCAS DEL TORO: vicinity Chiriquí Lagoon, *von Wedel 2096.*

A very common lowland species widely distributed in Central America. It seems probable that it may represent a northern variant of the generic type, *Trigonidium obtusum* Lindl. of British Guiana and Brazil, differing only in the narrower leaves and the absence of an apparently distinct verrucose callus on the under-surface of the apex of the lip.

2. TRIGONIDIUM LANKESTERI Ames, in Sched. Orch. 5:32. 1923.

Repent or scandent, epiphytic herbs with ovoid, compressed, ridged and sulcate, tapering pseudobulbs 4–8 cm. tall and 2–3 cm. wide at the base, very distantly spaced on the elongate, cylindric rhizome, the internodes 15–40 cm. long, enveloped in numerous tubular, papery bracts which weather away, the basal portion of the pseudobulbs freely rooting and covered by several rigid, imbricating sheaths which soon weather into loose fibers, the apex of the pseudobulbs with 3–5 leaves. Leaves subcoriaceous, oblong-lanceolate, acute, 15–27 cm. long and 3–4 cm. wide, contracted below into slender, conduplicate petioles which are more or less distichously arranged on the apex of the pseudobulbs. Inflorescences short, usually solitary, 1-flowered scapes 8–16 cm. long, produced from the bases of the pseudobulbs. Sepals subequal, free, the basal half, together with the petals, connivent

and forming a tube, the petals visible between the margins of the dorsal and lateral sepals, the apical half of the sepals strongly reflexed, light greenish tan to cinnamon, veined brown or purplish, elliptic-oblanceolate, acute, 4.5–5 cm. long and 1.6–2 cm. wide, the dorsal sepal a little narrower than the laterals. Petals broadly oblanceolate, the apices abruptly spreading and conspicuously apiculate or aristate, light greenish tan, veined brown, with purple spots, 20–24 mm. long and 8–10 mm. wide, with an irregular subventricose swelling on the inside below the apicule. Lip 3-lobed, white spotted brown, about 15 mm. long and 5 mm. wide, oblanceolate when spread out, the base contracted and articulated with the base of the column, the lateral lobes erect in natural position, the triangular acute apices projecting, the mid-lobe ovate, obtuse, fleshy, strongly recurved, about ½ the total length of the lip, the upper-surface minutely glandular, the under-surface strongly verrucose, the disk with a ligular, fleshy callus about equaling the lateral lobes in length. Column semiterete, somewhat arcuate, about 1 cm. long, the base without a foot.

Costa Rica and Panama.

COCLÉ: hills north of El Valle de Antón, 800–1000 m., *Allen 2290*.

An exteremely distinctive highland species, immediately separable from the common lowland *Trigonidium Egertonianum* by the elongate rhizome, the 3- to 5-leaved pseudobulbs, the larger flowers, and the apiculate petals.

67. CRYPTOCENTRUM Benth.

CRYPTOCENTRUM Benth. in Jour. Linn. Soc. 18:325. 1881, nom. nud.; Benth. & Hook. Gen. Pl. 3:557. 1883.

Pittierella Schltr. in Fedde Rep. Sp. Nov. 3:80. 1906.

Small erect, epiphytic herbs with 1 to several short stems, usually without pseudobulbs, the cylindric basal portions of the stems enveloped in the rigid, persistent leaf bases. Leaves approximate, 2-ranked, linear to ligular, coriaceous, usually confined to the upper portions of the stems. Inflorescences few to numerous, slender, erect or arching, 1-flowered scapes produced from the bases of the plants, usually less than (but sometimes exceeding) the leaves, the peduncles enveloped in tubular, acute or acuminate, papery sheaths, the uppermost of which is much the longest, completely covering the ovary, only the perianth segments of the flowers being exserted. Flowers relatively small. Sepals narrow, the free portions widely spreading, the dorsal sepal usually a little shorter than the laterals, the bases of which are connate and produced into a long, narrow spur which is appressed to the ovary and nearly equaling it in length. Petals subequal to the dorsal sepal or smaller. Lip continuous with the base of the column, produced into an elongate tubular projection contained within, and nearly equaling the sepaline spur, the free limb entire or more or less divided into a basal and an apical half, the basal half concave to subsaccate, the erect lateral margins enclosing

the column, the apical half usually lanceolate or elliptic-lanceolate and spreading. Column short, very stout, wingless but with the apex usually with a pair of lateral auricles covering the clinandrium, the base without a foot. Anther terminal, operculate, incumbent, 1-celled; pollinia 2–4, waxy.

A small genus of tropical American highland epiphytes, ranging from Costa Rica to Peru. Until more adequate collections are available for study, it would be profitless to speculate on the possible number of valid entities. Although the described species vary considerably in size, the flowers of most seem to be remarkably constant in structure, so that many of the names may eventually be reduced to synonymy or some perhaps retained as local varieties of a few somewhat polymorphic species. Four entities are separable in Panama, largely on a basis of size and vegetative habit.

a. Plants less than 3 cm. tall. Inflorescences conspicuously exceeding the leaves..... 4. C. STANDLEYI
aa. Plants more than 6 cm. tall. Inflorescences less than, or barely equaling the leaves.
  b. Plants 6–12 cm. tall. Leaves 3.5 mm. wide or less. Spur 1.2–2.0 cm. long..... 1. C. GRACILIPES
  bb. Plants more than 12 cm. tall. Leaves 3.5 mm. wide or more. Spur about 3 cm. long.
    c. Leaves narrowly linear, acuminate..... 2. C. INAEQUISEPALUM
    cc. Leaves broadly ligular, unequally emarginate..... 3. C. LATIFOLIUM

1. CRYPTOCENTRUM GRACILIPES Schltr. in Fedde Rep. Sp. Nov. Beih. 19:246. 1923.

Erect, usually caespitose, epiphytic herbs without pseudobulbs, the plants 6–12 cm. tall. Leaves coriaceous, spreading, approximate, linear-ligular, the apices obtuse or unequally emarginate, 5–10 cm. long and 0.2–0.5 cm. wide, the sheathing bases contracted into short cylindric petioles. Inflorescences numerous slender, erect or arching, 1-flowered scapes usually nearly equaling the leaves in length, enveloped throughout in several papery, tubular, imbricating sheaths. Flowers small, tan or brownish olive. Sepals oblong, obtuse, widely spreading, the free portions 10–13 mm. long and 2.5–3 mm. wide, the laterals oblique and rather narrower than the dorsal sepal, the bases connate and produced into an elongate spur 1.2–2 cm. long, parallel with the ovary and about equaling it in length. Petals obliquely elliptic-lanceolate, acute, 8–10 mm. long and 2–2.5 mm. wide. Lip entire, the free limb lanceolate, obtuse to subacute, 6–8 mm. long and 2.5–3 mm. wide, the base continuous with the base of the column and produced into a long narrow tube which is contained within the elongate, sepaline spur. Column short, stout, about 2 mm. long, the base footless.

Costa Rica and Panama.

COCLÉ: hills north of El Valle de Antón, 1000 m., *Allen 1911*.

2. CRYPTOCENTRUM INAEQUISEPALUM C. Schweinf. in Bot. Mus. Leafl. Harv. Univ. 12:186. 1946.

Erect, epiphytic herbs without pseudobulbs, the plants 15–25 cm. tall, the short, cylindric stems enveloped below in the persistent leaf bases, the apical por-

tions with 2-ranked foliage. Leaves approximate, linear, acuminate, coriaceous, 12–23 cm. long and 0.35–0.6 cm. wide. Inflorescences numerous slender, 1-flowered scapes produced from the base of the stem, the peduncles entirely invested by several papery, tubular sheaths. Flowers relatively large for the genus, described as being greenish yellow and translucent. Sepals widely spreading above, lanceolate, acute, the dorsal sepal about 15 mm. long and 3.7 mm. wide, the lateral sepals oblique, the free parts about 19 mm. long and 3 mm. wide, the bases connate and produced into an elongate spur which is closely appressed to and about equaling the ovary in length. Petals obliquely lanceolate, acuminate, about 13 mm. long and 3 mm. wide. Lip continuous with the base of the column, the free limb ovate-lanceolate, acute to acuminate when spread out, about 10 mm. long and 4.2 mm. wide, the lower half deeply concave to subsaccate in natural position, the lateral margins enclosing the column, the base produced into a long slender tube contained within the sepaline spur. Column very short, stout, about 2 mm. long, the clinandrium shielded by 2 broad lateral auricles, the base without a foot.

Panama and Peru. To be expected in Colombia and Ecuador.

CHIRIQUÍ: vicinity Bajo Chorro, headwaters of the Río Caldera, in rain forest, 6000 ft., *Davidson 160*.

Our specimens have thicker leaves, but in other respects seem to agree with the Peruvian type.

3. CRYPTOCENTRUM LATIFOLIUM Schltr. in Fedde Rep. Sp. Nov. Beih. 19:247. 1923.

Erect, epiphytic herbs without pseudobulbs, the plants 18–25 cm. tall, the short cylindric stems often solitary and apparently monopodial, enveloped below in the rigid, brown, persistent, imbricating leaf bases. Leaves approximate, spreading, broadly ligular, coriaceous, 16–23 cm. long and 1.5–2 cm. wide, the apices rounded and unequally emarginate. Inflorescences a few erect or arching, 1-flowered scapes 8–16 cm. long, produced from the bases of the stems, the peduncles completely invested by several acute, tubular, papery sheaths. Flowers relatively large, rather fleshy, greenish olive or greenish tan. Sepals widely spreading above, the free portions narrowly ligular-lanceolate, acute, 3.5–5 cm. long and 0.5–0.6 cm. wide, the margins often strongly revolute, the lateral sepals oblique, the bases connate and produced into an elongate spur which is closely appressed to the ovary and about equaling it in length. Petals obliquely lanceolate, acute, 3–4 cm. long. Lip continuous with the base of the column, the free portion lanceolate, subacute, about 1.5 cm. long and 0.5 cm. wide, the base produced into an elongate tube which is contained within the sepaline spur, as in the genus. Column short, stout, about 4 mm. long.

Costa Rica and Panama.

COCLÉ: region north of El Valle de Antón, vicinity La Mesa, 1000 m., *Dunn s. n.* (under *Allen 2762*).

A curious highland species, vegetatively reminiscent of a small *Aerides* or *Vanda*. Our specimen has somewhat smaller measurements than those given for the Costa Rican type, but otherwise seems nearer to it than to any other. Sterile plants of evidently the same species are fairly frequent on the eastern slopes of Chiriquí Volcano between 5000 and 7000 ft.

4. CRYPTOCENTRUM STANDLEYI Ames, in Sched. Orch. 9:55. 1925.

Dwarf, epiphytic herbs without pseudobulbs, the tufted plants less than 3 cm. tall. Stems cylindric, rather stout, the lower half covered by the persistent, imbricating leaf bases, the upper half with approximate, more or less 2-ranked foliage. Leaves narrowly linear to oblanceolate, obtuse to subacute, often conduplicate, coriaceous, 5–15 mm. long and 1–2.5 mm. wide. Inflorescences usually 1–2 erect, filiform, 1-flowered scapes 3–4 cm. long, produced from the lower axils of the leaves and conspicuously exceeding the foliage in height. Flowers small, dull red or tan. Sepals spreading, the free portions elliptic-lanceolate, acute, 6–8 mm. long and 1.5–2 mm. wide, the laterals connate at the base and produced into an elongate, slender spur which is closely appressed to the ovary and about equaling it in length. Petals lanceolate, acute, 5–7 mm. long and 1.5–2 mm. wide. Lip continuous with the base of the column, the free portion strongly concave, lanceolate, acute, 6–8 mm. long and about 2 mm. wide, the base prolonged into a slender tube contained within the sepaline spur. Column 2.2–2.5 mm. long, the apex with two lateral auriculate projections.

Costa Rica and Panama.

COCLÉ: hills north of El Valle de Antón, 600–1000 m., *Allen 1685*.

68. TRICHOCENTRUM Poepp. & Endl.

TRICHOCENTRUM Poepp. & Endl. Nov. Gen. & Sp. 2:11, *t. 115*. 1837[1]; Benth. & Hook. Gen. Pl. 3:559. 1883.

Acoidium Lindl. in Bot. Reg. 23: *t. 1951*. 1837, nom. nud.

Small, epiphytic herbs with very short, monophyllous stems which are thickened into short, inconspicuous pseudobulbs. Leaves elliptic-lanceolate to ligular, coriaceous or fleshy. Inflorescences usually simple, rarely branching, 1- or rarely 2-flowered scapes, usually very short, but sometimes nearly equaling the leaves. Flowers of moderate size to relatively large. Sepals subequal, free, spreading. Petals subequal to the sepals. Lip entire or obscurely 3-lobed, produced at the base into a spur. Column stout or slender, erect, the apex clavate or with prominent lateral wings or auricles, the base without a foot. Anther terminal, operculate, incumbent, 1-celled, often pubescent or papillose; pollinia 2, waxy.

Perhaps fifteen species of tropical American epiphytes, ranging from Mexico to Peru and Brazil. One species is known from Panama.

[1] The date of publication appearing on the title page of this volume is 1838, but evidently parts of it must have been published or in some way available for use earlier since Lindley (in Bot. Reg. 23: *t. 1951*, April 1, 1837) cited the generic name *Trichocentrum* and the place of publication.

1. Trichocentrum panamense Rolfe, in Kew Bull. 341. 1913.

Dwarf, epiphytic herbs with minute, monophyllous pseudobulbs, the plants 3–12 cm. tall. Leaves elliptic-lanceolate to ligular, acute, fleshy, 2.5–10 cm. long and 0.8–2.5 cm. wide. Inflorescences slender, horizontal or pendulous, usually unbranched scapes 0.8–4 cm. long, which apparently elongate by progressive stages, producing a succession of moderate-sized solitary flowers. Sepals subequal, free, spreading, pale green or greenish yellow, lanceolate, acute, 10–12 mm. long and 3–4 mm. wide. Petals pale green or greenish-yellow, oblong-lanceolate, acute, 10–12 mm. long and 3–4 mm. wide. Lip elliptic-ovate, obtuse to acute, explanate or concave, white with a reddish-brown or reddish-purple blotch at the base, the free portion 10–12 mm. long and about 6 mm. wide, the base adnate to the base of the column and produced into a broad, flattened, rather obscurely 4-lobed spur. Column stout, about 5 mm. long, the apex with a pair of broad, fleshy, spreading, subfalcate, obtuse wings on either side of the clinandrium, the base without a foot. Anther white, papillose.

Panama.

Canal Zone: trail from Fort Sherman to the mouth of the Río Chagres, sea level, *Powell 371*; upper Río Chagres, sea level, *Powell 419*. Panamá: Cerro Campana, vicinity Campana, 600–800 m., *Dorothy Allen 3989, 4455*. Coclé: lower valley and marshes along the Río Antón, 500–600 m., *Hunter & Allen 384, Dorothy Allen 3953, 5077*.

This species is very variable in regard to the size and shape of the leaves, and the length of the inflorescences.

69. IONOPSIS HBK.

Ionopsis HBK. Nov. Gen. & Sp. 1:348, *t. 83*. 1815; Benth. & Hook. Gen. Pl. 3:567. 1883.

Inopsis Steud. Nom. ed. 1, 432. 1821.
Iantha Hook. Exot. Fl. 2: *t. 113*. 1825.
Cybelion Spreng. Syst. 3:679. 1826.

Epiphytic herbs with short, subcylindric stems invested in 2-ranked foliage, the sheathing leaf bases with or without minute pseudobulbs. Leaves approximate, narrow, coriaceous, the bases imbricating. Inflorescences 1–3 slender, short to elongate, erect or arching, simple or paniculate scapes subterminal or lateral from the axils of the leaves. Flowers of moderate size to small. Sepals subequal, erect or spreading, the dorsal sepal free, the laterals connate at the base and produced into a short sac below the lip. Petals subequal to the dorsal sepal or broader. Lip clawed and adnate to the base of the column, the apical portion broadly expanded, entire or emarginate, conspicuously exceeding the sepals. Column short, stout, erect, the lateral margins not winged, the base without a foot. Anther terminal, operculate, incumbent, 1-celled or imperfectly 2-celled; pollinia 2, waxy.

A small genus of American epiphytes, ranging from Florida and Mexico through Central America and the West Indies to South America, as far as Bolivia and Paraguay. One species is known from Panama.

Fig. 187. *Ionopsis utricularioides*

1. Ionopsis utricularioides (Sw.) Lindl. Coll. Bot. *t. 39-A.* 1821.

Epidendrum utricularioides Sw. Prodr. 122. 1788.
Dendrobium utricularioides Sw. in Nov. Act. Soc. Upsal. 6:83. 1799.
Iantha pallidiflora Hook. Exot. Fl. 2: *t. 113.* 1824.
Ionopsis tenera Lindl. in Bot. Reg. 22: *t. 1904.* 1836.
Ionopsis pallidiflora Lindl. loc. cit. sub. *t. 1904.* 1836.
Ionopsis paniculata Lindl. loc. cit. 1836.
Ionopsis zonalis Lindl. & Paxton, in Paxton's Flow. Gard. 2:13. 1851–53, in textu.

Epiphytic herbs 5–12 cm. tall. Leaves approximate, linear-lanceolate to oblong-lanceolate, acute, the blades 3.5–12 cm. long and 0.5–1.5 cm. wide, the midvein forming a keel on the under-surface, the sheathing bases sometimes enveloping a minute pseudobulb. Inflorescences 1–3 slender, erect or arching, simple or paniculate scapes 15–60 cm. long, produced from the lateral or subterminal leaf axils, provided with a few distant, inconspicuous sheaths. Flowers few to many, small to relatively large and conspicuous, lavender, rose-purple, or white, superficially resembling those of some species of *Utricularia.* Sepals subequal, not spreading, oblong-lanceolate to elliptic-lanceolate, acute, 3–6 mm. long and 1–2 mm. wide, the dorsal sepal free, concave, the laterals connate at the base and produced into a short, broad, obtuse sac. Petals subequal to the dorsal sepal, elliptic-ovate, acute, or obtuse and shortly apiculate, 2.5–5 mm. long and 1.5–3 mm. wide. Lip about twice as long as the sepals, 5–12 mm. long and 5–12 mm. wide, the apex broadly spreading, deeply emarginate and 2-lobed, contracted at the base into a fleshy, biauriculate claw which is adnate to the base of the column, the apex of the claw with 2 suborbicular, flattened calli. Column short, rather stout, without wings, about 2 mm. long, the base without a foot.

Mexico to Brazil and Paraguay; Florida; West Indies.

CANAL ZONE: vicinity Gamboa, 100 ft., *Dorothy Allen 4572.* PANAMÁ: hills east of Panama City, sea level, *Powell 181.*

A common epiphyte widely distributed throughout the lowlands of the American tropics and sub-tropics. The species is very variable in regard to the size of flowers and width of leaves.

70. RODRIGUEZIA Ruiz & Pavon

Rodriguezia Ruiz & Pavon, Fl. Peruv. & Chil. Prodr. 115, *t. 25.* 1794; Benth. & Hook. Gen. Pl. 3:559. 1883.

Burlingtonia Lindl. in Bot. Reg. 23: *t. 1927.* 1837.
Physanthera Bert. ex Steudel, Nom. ed. 2, 2:330. 1841, nom. nud.

Epiphytic herbs with short, ovoid or elliptic-oblong, compressed, 1- to 2-leaved pseudobulbs distantly inserted on an elongate rhizome, or approximate, usually almost completely hidden by the conduplicate, imbricating bases of 2 to several conspicuous, foliaceous bracts. Leaves of the apex of the pseudobulbs and the blades of the foliaceous bracts coriaceous, ligular to elliptic-lanceolate, obtuse to

acute, or unequally emarginate. Inflorescences 1 to several simple, erect or deflexed racemes, produced from the axils of the foliaceous bracts. Flowers few to many, of moderate size to relatively large and conspicuous. Sepals usually dissimilar, the dorsal sepal free, concave and petaloid, the laterals usually connate for their entire length, forming a single conduplicate segment below the lip, often strongly geniculate or gibbose when seen in profile, or rarely connate for only about half their length, with the acute apices spreading. Petals subequal to the dorsal sepal. Lip usually exceeding the sepals, the base clawed, continuous with the base of the column and produced into a short spur or gibbose projection which is appressed to the ovary, the claw parallel with the column, the free limb spreading, obovate or obcordate, the disk often cristate. Column erect, slender, subcylindric, the apex dilated or subclavate, often with variously shaped arms or auricles, the base without a foot. Anther terminal, operculate, incumbent, 1-celled; pollinia 2, waxy.

A small genus of attractive tropical American epiphytes, ranging from Costa Rica to Peru and Brazil. Two species are known from Panama.

a. Inflorescences erect, equaling or exceeding the leaves. Sepals about 1 cm. long..... 2. R. SECUNDA
aa. Inflorescences deflexed, not equaling the leaves. Sepals about 2.5 cm. long..... 1. R. COMPACTA

1. RODRIGUEZIA COMPACTA Schltr. in Fedde, Rep. Sp. Nov. Beih. 19:144. 1923.

Epiphytic herbs with oblong-elliptic, compressed, monophyllous pseudobulbs 1.5–2.5 cm. long and 1.0–1.5 cm. wide, nearly hidden by the conduplicate imbricating bases of several conspicuous, foliaceous bracts. Leaves from the apex of the pseudobulbs and the blades of the foliaceous bracts oblong-ligular to ligular, coriaceous, the apices obtuse or obscurely emarginate, 6–14 cm. long and 1.5–2.5 cm. wide. Inflorescences 1–2 lax, slender, deflexed, few-flowered racemes 3–4.5 cm. long. Flowers of moderate size, conspicuously larger than those of *Rodriguezia secunda*, pale yellow or greenish yellow with a yellow lip. Sepals dissimilar, the dorsal sepal narrowly oblong, obtuse, concave, about 2.5 cm. long, the laterals connate for their entire length, forming a single conduplicate segment below the lip, about 2.6 cm. long, the apex shortly bifid, the base geniculate in profile. Petals obliquely oblong, obtuse, about 2.5 cm. long. Lip adnate to the foot of the column, about 2.5 cm. long and 1 cm. wide, the free limb obovate-spatulate, the apex deeply emarginate and 2-lobed, the mid-nerve thickened and projecting between the apical lobes as a short apicule, the base produced into a short, curved, subulate spur. Column subcylindric, the apex dilated and subclavate, with projecting arms, the basal half minutely puberulent, the base without a foot.

Costa Rica and Panama.

BOCAS DEL TORO: Río Cricamola, between Finca St. Louis and Konkintöe, about 10–50 m., *Woodson 1888*.

An apparently attractive species, readily separable from the common *Rodriguezia secunda* by the short, deflexed inflorescences and the relatively large, greenish white or pale yellow flowers.

2. RODRIGUEZIA SECUNDA HBK. Nov. Gen. & Sp. 1:367, *t. 92.* 1816.

Pleurothallis coccinea Hook. Exot. Fl. 2: *t. 129.* 1815.
Rodriguezia lanceolata Lodd. Bot. Cab. 7: *t. 676.* 1822, non *R. lanceolata* R. & P.
Rodriguezia secunda HBK. var. *panamensis* Schltr. in Fedde, Rep. Sp. Nov. Beih. 17:75. 1922.

Erect, epiphytic herbs with oblong-elliptic, compressed, monophyllous pseudobulbs 2–3.5 cm. long and 1.0–1.6 cm. wide, almost completely covered by the conduplicate, imbricating bases of the 4–7 conspicuous, foliaceous bracts. Leaves of the apex of the pseudobulbs and the blades of the foliaceous bracts coriaceous to rather fleshy, linear-ligular to elliptic-oblong, obtuse, subacute or unequally emarginate at the apex, 7–24 cm. long and 1–3.5 cm. wide. Inflorescences 1–6 erect or arching, unbranched, unilateral racemes 15–38 cm. tall. Flowers many, rather small, pink to rose-red. Sepals dissimilar, not spreading, the dorsal sepal concave, ovate, obtuse with a minute apicule, or subacute, 9–12 mm. long and 5–6 mm. wide, the lateral sepals connate for their entire length, forming a single, conduplicate segment below the lip, 10–15 mm. long, the base conspicuously gibbose or geniculate when seen in profile. Petals obovate, shortly acute or apiculate, 9–12 mm. long and 6–7 mm. wide. Lip entire, obscurely clawed, the biauriculate claw adnate to the base of the column and produced into a very short spur, the free limb oblong-obovate, with undulate margins, 12–15 mm. long and 5–7 mm. wide, the apex deeply emarginate and 2-lobed, the disk with a prominent fleshy bicarinate callus. Column subcylindric, the apex rather dilated and subclavate, with 2 short projecting teeth on the under-side.

Panama, Colombia, Venezuela, British Guiana, Surinam, and Trinidad.

CANAL ZONE: vicinity Frijoles, sea level, *Powell 3184;* along Río Chagres, between Gamboa and Alahuela, 30–60 m., *Allen 962;* Gatún Lake, sea level, *Powell s. n.* PANAMÁ: hills east of Panama City, *Powell s. n.;* vicinity Paja, near Empire, sea level, *Powell 3194;* vicinity Juan Mina, Río Chagres, 100 ft., *Allen & Allen 4133.* COLÓN: Cativo-Porto Bello trail, sea level, *Powell s. n.*

71. TRIZEUXIS Lindl.

TRIZEUXIS Lindl. Collect. Bot. *t. 2.* 1823; Benth. & Hook. Gen. Pl. 3:566. 1883.

Trixeuxis Lindl. Orch. Sel. 15. 1826.

Small epiphytic herbs with short, distichous, foliaceous stems, the imbricating leaf bases distichously arranged in the form of an open fan and usually enveloping a small, monophyllous pseudobulb. Leaves falcate to gladiate, acute. Inflorescences paniculate scapes produced from the bases of the pseudobulbs and conspicuously exceeding the leaves. Flowers subglobose, minute, in dense racemes terminating the branches of the panicle. Sepals dissimilar, of about equal length, the dorsal sepal arching, deeply concave, the laterals connate for nearly their entire length, forming a single bifid segment below the lip. Petals elliptic-ovate, obtuse or subacute, about as long as the sepals. Lip entire, concave, articulated with the

base of the column, the lateral margins erect and parallel with the column, the apex rather fleshy and recurved. Column subcylindric, erect, the base without a foot. Anther terminal, operculate, incumbent, 1-celled; pollinia 2, waxy.

Two or three species of small American epiphytes ranging from Costa Rica to Trinidad, Brazil, Bolivia, and Peru. One species is known from Panama.

1. TRIZEUXIS FALCATA Lindl. Collect. Bot. *t. 2.* 1823.

Trizeuxis andina Schltr. in Fedde, Rep. Sp. Nov. Beih. 10:52. 1922.

Small to minute, erect, epiphytic herbs 2.5–10 cm. tall, with short, distichous, foliaceous stems, the imbricating leaf bases usually enveloping a small, subquadrate, compressed, monophyllous pseudobulb. Leaves falcate or gladiate, acute or acuminate, the complanate blades 1.5–8 cm. long and 0.3–1.0 cm. wide, the imbricating bases distichously arranged in the form of an open fan. Inflorescences slender, erect, paniculate scapes 3–20 mm. long, produced from the bases of the pseudobulbs, conspicuously exceeding the leaves. Flowers subglobose, minute, in dense, subcapitate or elongate racemes terminating the branches of the panicle. Sepals dissimilar, of about equal length, green or pale yellow, the dorsal sepal ovate, acute, arching and deeply concave, about 2 mm. long, the laterals connate for nearly their entire length, forming a single obovate, bifid segment about 2 mm. long below the lip. Petals elliptic-ovate, obtuse or subacute, about as long as the sepals. Lip entire, lanceolate, acute, about 2.5 mm. long, the base concave, the lateral margins erect and closely appressed to the sides of the column, the apex rather fleshy and recurved, ovate, acute, yellow or orange, about ⅓ the total length of the lip. Column short, stout, subcylindric, about 1 mm. long, the apex somewhat dilated, the base without a foot. Anther very large in proportion to the size of the flower, about 1.2 mm. long.

Costa Rica, Panama, Venezuela, Trinidad, Brazil, Bolivia, and Peru.

VERAGUAS: vicinity Santiago, 700 ft., *Powell 3526.* CHIRIQUÍ: vicinity Concepción, 800 ft., *Powell 286.*

72. TRICHOPILIA Lindl.

TRICHOPILIA Lindl. Nat. Syst. Bot. ed. 2, 446. 1836; Benth. & Hook. Gen. Pl. 3:559. 1883.

Pilumna Lindl. in Bot. Reg. n. s. 7: Misc. 73. 1844.
Helcia Lindl. loc. cit. 8: Misc. 17. 1845.
Leucohyle Klotzsch, in Ind. Sem. Hort. Bot. Berol. App. 1. 1854.
Trichophila Pritz. Icon. Bot. Ind. 1115. 1855, sphalm.

Erect epiphytic herbs with approximate monophyllous pseudobulbs. Leaves subcoriaceous to coriaceous or sometimes fleshy, usually elliptic-lanceolate to ligular, rarely narrowly linear or semiterete. Inflorescences slender, short or elongate, erect, arching or pendulous, 1- to 7-flowered scapes produced from the bases of the pseudobulbs. Flowers usually large and attractive. Sepals narrow,

widely spreading, often twisted, usually subequal and free, the laterals sometimes connate at the base, rarely as far as the middle. Petals subequal to the dorsal sepal. Lip entire or 3-lobed, clawed at the base and adnate to the base of the column, the limb spreading or the lateral lobes convolute and forming a tube, the mid-lobe spreading, the disk smooth or lamellate. Column erect, semiterete, the margins of the apex projecting, entire or lobed, usually dentate or fimbriate, the base of the column without a foot. Anther terminal within the clinandrium, operculate, incumbent, 1-celled; pollinia 2, waxy.

A small genus of tropical American epiphytes ranging from southern Mexico to Peru, Brazil, and the West Indies. It is another of the frequently recurring and perplexing instances in which the specific concepts within the genus are by no means of equal value. In this case there are several groups of closely related entities, each group centering on an archetypal species, and more closely related to it, and each to the other, than to other similar groups within the genus. For example, *Trichopilia subulata* is obviously closely allied to, if not actually identical with *T. mutica;* and both markedly distinct from the archetype *T. suavis,* and its associate *T. leucoxantha,* or from the archetype *T. tortilis,* with its closely allied species *T. marginata, T. maculata, T. turialbae, T. Galeottiana,* etc. Due to the lack, in most instances, of types or adequate series upon which to base comparative studies, I hesitate at this time to undertake any such wholesale overhauling of names as would seem to be required on the basis of probable relationships. The present treatment, for the most part, follows established usage, but it is to be expected that many of these minor concepts may ultimately be reduced to varietal status or synonymy. At the present time six separable specific concepts are represented in Panama.

a. Pseudobulbs subcylindric. Leaves fleshy, narrowly linear to semiterete, 10 mm. wide or less. Lip not tubular ..... 5. T. SUBULATA
aa. Pseudobulbs ancipitous, linear to suborbicular. Leaves coriaceous to subcoriaceous, ligular to elliptic-lanceolate, 15 mm. wide or more. Lip tubular.
  b. Pseudobulbs linear, usually more than 4 times as long as broad.
    c. Lateral sepals connate to about the middle ..... 6. T. TURIALBAE
    cc. Lateral sepals not connate at the base ..... 3. T. MARGINATA
  bb. Pseudobulbs elliptic-oblong to suborbicular, less than 3 times as long as broad.
    c. Leaves 2–3.5 cm. wide. Basal imbricating bracts of the pseudobulbs conspicuously maculate. Scapes 1-flowered, the inner lip with an inconspicuous keel not equaling the column in length ..... 2. T. MACULATA
    cc. Leaves 4–7 cm. wide. Basal imbricating bracts of the pseudobulbs not maculate. Scapes several-flowered, the inner lip with a prominent central keel equaling or exceeding the column in length.
      d. Sepals 2.5–3.5 cm. long ..... 1. T. LEUCOXANTHA
      dd. Sepals 4–6 cm. long ..... 4. T. SUAVIS

1. TRICHOPILIA LEUCOXANTHA L. Wms. in Am. Orch. Soc. Bull. 10:137. 1941.

Erect, epiphytic herbs 20–25 cm. tall, with approximate, elliptic-oblong to suborbicular, compressed, monophyllous pseudobulbs 2.5–4.5 cm. long and 2–3.5 cm. wide, the bases enveloped in several thin, papery, imbricating bracts which

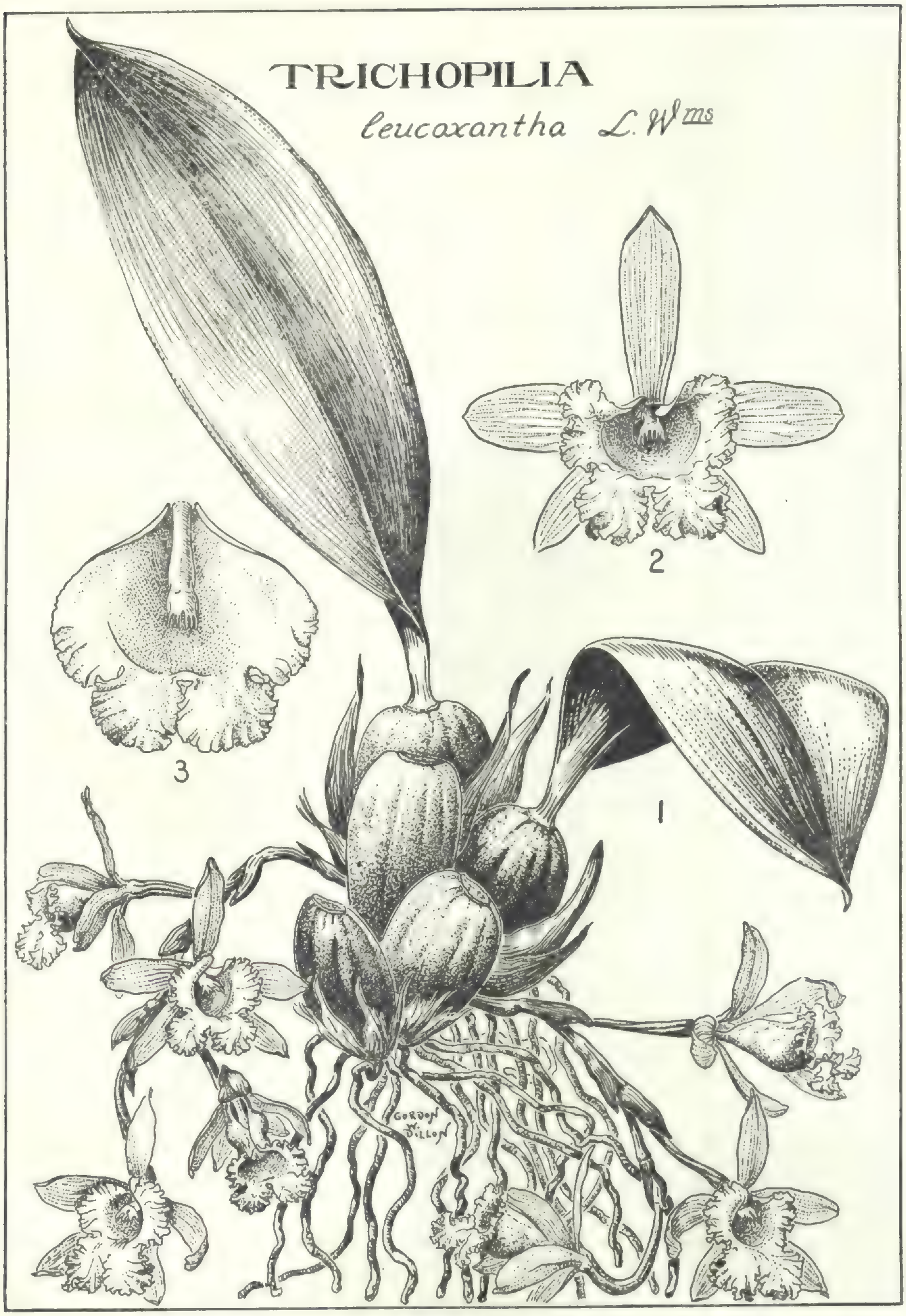


Fig. 188. *Trichopilia leucoxantha*

soon weather away. Leaves elliptic-lanceolate, acute, subcoriaceous, 15–20 cm. long and 4–6 cm. wide, contracted at the base into a short, conduplicate petiole. Inflorescences arching or pendulous, 1- to 4-flowered scapes 5–7 cm. long, produced from the bases of the pseudobulbs. Flowers of moderate size, white with a pale yellow blotch at the base of the lip. Sepals free, spreading, the dorsal sepal oblanceolate, acute, 2.5–3.5 cm. long and 0.7–0.8 cm. wide, the laterals lanceolate, acute, 2.5–3 cm. long and 0.6–0.8 cm. wide. Petals subequal to the dorsal sepal, elliptic-oblong, obtuse with a minute apicule, 2.5–3.2 cm. long and 0.9–1.0 cm. wide. Lip 3-lobed, broadly obovate when spread out, 3–3.5 cm. long and 3–3.5 cm. wide, the narrow base adnate to the base of the column, the lateral lobes rounded, incurving over the column, the anterior margins more or less undulant, the mid-lobe spreading or reflexed, deeply emarginate, the lateral lobules strongly undulate, the disk with a prominent central keel about equaling the column in length. Column slender, terete, 15–18 mm. long, the margins of the apex projecting and forming a fimbriate hood over the anther, the base of the column without a foot.

Panama.

COCLÉ: western slope and summit of Cerro Valle Chiquito, 700–800 m., *Seibert 515;* vicinity El Valle de Antón, 600–1000 m., *Allen 2401, 3564;* floor of El Valle, 600 m., *Fairchild s. n.*

Thus far known only from the region of El Valle de Antón, in Coclé Province. The plants considerably resemble those of *Trichopilia suavis*, and may possibly represent only a small-flowered variety of that species.

2. TRICHOPILIA MACULATA Rchb. f. in Bonplandia 3:215. 1855.

Trichopilia Powellii Schltr. in Fedde, Rep. Sp. Nov. Beih. 17:77. 1922.

Dwarf, epiphytic herbs; pseudobulbs elliptic-oblong, strongly ancipitous, 1-leaved, 2–5 cm. long and 1.5–2.5 cm. wide, approximate and inserted at an acute angle on the short rhizome, the bases enveloped in several densely spotted, imbricating, papery bracts. Leaves elliptic-lanceolate, acute, subcoriaceous, 5–12 cm. long and 2–3.5 cm. wide. Inflorescences usually solitary, slender, arching or semipendulous 1-flowered scapes 4–6 cm. long, produced from the bases of the pseudobulbs. Flowers of moderate size. Sepals subequal, free, widely spreading, lanceolate, acuminate, often somewhat twisted, pale yellow or greenish yellow, 3–4 cm. long and 0.35–0.5 cm. wide. Petals subequal to the sepals, lanceolate, acuminate, pale or greenish yellow, about 3.5 cm. long and 0.5–0.6 cm. wide, often with undulant margins. Lip obscurely 3-lobed, obovate when spread out, about 3.5 cm. long and 1.6–1.8 cm. wide, contracted at the base and adnate to the base of the column, white, aging pale yellow, the inner lip yellow with numerous fine orange-red lines, the rounded lateral margins convolute, forming a tube, the mid-lobe emarginate, with spreading or reflexed lobules, the disk with a short, inconspicuous, central keel not equaling the column in length. Column slender,

Fig. 189. *Trichopilia maculata*

semiterete, the margins of the apex distinctly 3-parted and minutely denticulate, forming a hood over the anther.

Panama.

CANAL ZONE: vicinity Salamanca Hydrographic Station, upper Madden Lake region, 70–80 m., *Dodge, Steyermark & Allen s. n.;* Balboa, sea level, *Powell 3422;* drowned forest along Río Chagres, Madden Lake region, 66 m., *Steyermark & Allen 16770;* Barro Colorado Island, Gatún Lake, *Shattuck 555;* San Jose Island, Perlas Archipelago, *Johnston 148, 1276.* PANAMÁ: hills near Panama City, *Powell 3096;* Orange River valley, 75 m., *Killip 3247;* vicinity La Chorrera, 20 m., *Allen 2842;* Río La Maestra, 0–25 m., *Allen 51.*

Small, but attractive plants fairly frequent in the lowlands of the central and eastern Isthmian area. The species apparently is confined to Panama. Guatemalan specimens identified as this species seem more readily referable to the Mexican *T. tortilis.*

3. Trichopilia marginata Henfr. in Gard. Mag. Bot. 3:185. 1851.

Trichopilia coccinea Warscz. in Paxton's Flow. Gard. 2:79. 1851-52.
Trichopilia crispa Lindl. in Gard. Chron. 342. 1857.
Trichopilia lepida Hort. ex Flor. Mag. n. s. *t. 98*. 1874.

Erect, epiphytic herbs with approximate, linear, broadly truncate, strongly ancipitous, 1-leaved pseudobulbs 6–14 cm. long and 1–2.5 cm. wide, the bases enveloped in several imbricating, papery, usually conspicuously maculate sheaths. Leaves elliptic-lanceolate to lanceolate, acute to acuminate, coriaceous, 12–30 cm. long and 3–5.5 cm. wide, contracted at the base into very short, conduplicate petioles. Inflorescences short, arching or pendulous, 2- to 3-flowered scapes produced from the bases of the pseudobulbs. Flowers large and conspicuous, very variable in color, most frequently with the sepals and petals reddish with lighter margins, the lip usually white on the outer surface, rarely red, the inner tube a deep rose-red, the reflexed margins of the mid-lobe often margined white. Sepals narrow, subequal, free, widely spreading, lanceolate to oblanceolate, acute, usually not twisted but sometimes with undulant margins, 4.5–6 cm. long and 0.6–1.0 cm. wide. Petals subequal to the sepals, spreading, oblanceolate, acute, 4–5.5 cm. long and 0.8–1.2 cm. wide, often with undulant margins. Lip tubular at the base, the apex obovate when spread out, 5–8 cm. long and 4–5 cm. wide, the narrow base adnate to the base of the column, the lateral lobes rounded and convolute forming a tube, the mid-lobe deeply emarginate, the lateral lobules spreading or recurved, with undulant margins, the disk without a prominent keel. Column terete, the margins of the apex projecting, forming an obscurely 3-lobed, fimbriate hood over the anther.

Guatemala, Costa Rica, Panama, and Colombia.

Chiriquí: Caldera River flats, 3800 ft., *Powell 3333;* without definite locality, 4000 ft., *Powell 154, 3291;* forests around El Boquete, 1000–1300 m., *Pittier 2969;* in heavy forest along road below El Hato, s. w. slopes of Chiriquí Volcano, 3800 ft., *Allen s. n.*

A large-flowered, attractive species first collected by von Warscewicz in 1849 on the slopes of Chiriquí volcano and introduced into cultivation under the name of *Trichopilia coccinea.* The plants are fairly common in heavy forest at 3500–5500 ft. elevation, growing usually in dense shade on the lower trunks of the trees. They are strikingly similar to the earlier *T. tortilis* of Mexico and Guatemala, and it seems very probable that our plants represent at most a somewhat more robust variety of that species.

There are several well-marked color forms, of which the following are recorded from Panama.

Trichopilia marginata var. alba Rchb. f.

Flowers pure white, the inner lip lemon-yellow.

Trichopilia marginata var. lepida Veitch, Man. Orchid. Pl. 2^9:183. 1893.

Flowers somewhat larger than in the type; the sepals and petals blotched rose-

pink, as is also the frontal lobe of the lip; the sepals and petals with very broad white margins.

Fig. 190. *Trichopilia suavis*

Trichopilia marginata var. olivacea Rchb. f. Beitr. Orch. Centr.-Amer. 13. 1866.

Sepals and petals olive-green.

4. Trichopilia suavis Lindl. & Paxton in Paxton's Flow. Gard. 1:44. 1850-51.

Trichopilia Kienastiana Rchb. f. in Gard. Chron. n. s. 20:166. 1883.

Erect, epiphytic herbs with approximate, rather fleshy, oblong-ovoid, elliptic or suborbicular, laterally compressed, monophyllous pseudobulbs 3.5–8 cm. long and 2.5–6 cm. wide, the bases enveloped in several thin, papery, imbricating bracts which soon weather away. Leaves elliptic-lanceolate, acute, subcoriaceous, 10–40 cm. long and 3.5–8 cm. wide, contracted below into short or elongate, conduplicate petioles. Inflorescences short, arching or pendulous, 2- to 5-flowered scapes produced from the bases of the pseudobulbs. Flowers large and attractive, fragrant, the sepals and petals white or creamy white sometimes spotted with pale rose-pink or red, the lip white or creamy white usually heavily spotted rose-pink, the inner tube most frequently with yellow or orange markings, very rarely blotched red. Sepals subequal, free, widely spreading, usually with undulate margins, lanceolate, acute, with a central thickened nerve or keel on the dorsal surface, 3–5.5 cm. long and 0.6–1.0 cm. wide, the lateral sepals rarely somewhat connate at the very base. Petals subequal to the sepals, lanceolate, shortly acute, with undulate margins, 2.8–5 cm. long and 0.8–1.2 cm. wide. Lip tubular, 3-lobed, obovate when spread out, 4.5–6.5 cm. long and 3–5 cm. wide, the narrow base adnate to the base of the column, the rounded lateral lobes convolute forming a tube, the anterior margins usually crisped and undulate, the mid-lobe retuse or emarginate, the lobules undulate, crisped and reflexed, the disk with a prominent, erect, central keel exceeding the column in length. Column elongate, terete, the margins of the apex projecting, forming a conspicuous, fimbriate, obscurely 4-lobed hood over the anther.

Costa Rica, Panama, and Colombia.

Chiriquí: without definite locality, 4000–5500 ft., *Powell 135, 3334, 3342, 3348*; Llanos on southwest slope of Chiriquí Volcano and along Río Chiriquí Viejo, 1200 m., *Allen 912*.

This is one of the most attractive species of the genus. It was first discovered by von Warscewicz in 1848, very probably in Costa Rica; but by far the finest forms have been found on the slopes of Chiriquí volcano in Panama, where they are fairly common in low mossy woods at 3800–5500 ft. elevation. The fragrant flowers are variable in color, a pure white form being rather frequent. They are usually produced in March and April.

5. Trichopilia subulata (Sw.) Rchb. f. in Flora 48:278. 1865.

Epidendrum subulatum Sw. Prodr. 123. 1788.
Cymbidium subulatum Sw. in Nov. Act. Soc. Upsal. 6:73. 1799.
Leucohyle Warscewiczii Kl. in Ind. Sem. Hort. Bot. Berol. App. 1. 1854.

Fig. 191. *Trichopilia subulata*

Trichopilia hymenantha Rchb. f. in Bonplandia 2:90. 1854.
Trichopilia jamaicensis Fawc. & Rendle, in Jour. Bot. 48:107. 1910.
Leucohyle subulata (Sw.) Schltr. Die Orchideen, 469. 1914.

Small, caespitose, epiphytic herbs 10–25 cm. tall, with short, inconspicuous, approximate, subcylindric, monophyllous pseudobulbs 1–2.5 cm. long and 0.2–0.5 cm. wide, the bases enveloped in several brown, papery, imbricating sheaths. Leaves fleshy, linear-lanceolate to semiterete, acuminate, 9–22 cm. long and 0.3–1.0 cm. wide, contracted at the base and apparently continuous with the apices of the slender pseudobulbs. Inflorescences pendulous, unbranched racemes 2.5–6 cm. long, produced from the bases of the foliaceous stems. Flowers small for the genus, usually 3–8, on slender pedicels, each subtended by a broad, acute to acuminate, spathaceous, papery bract. Sepals subequal, free, spreading, pure white to pale yellow, linear-lanceolate, acuminate, 20–23 mm. long and 3–4 mm. wide.

Petals subequal to the sepals, spreading, linear-lanceolate, acuminate, pure white to pale yellow, 18–20 mm. long and 2.5–3 mm. wide. Lip entire to obscurely 3-lobed, concave, obovate to elliptic-oblong, abruptly acute, or obtuse and apiculate, the margins minutely denticulate to conspicuously lacerate, white, usually irregularly spotted rose-purple, 15–20 mm. long and 12–18 mm. wide, the base adnate to the base of the column, the lateral margins erect at the very base and somewhat incurving over the column, the limb spreading, the disk with a short, fleshy, bifid or bicarinate callus. Column semiterete, 7–9 mm. long, the margins of the apex projecting, forming an entire, denticulate to fimbriate hood over the anther, the sides of the clinandrium below the hood with a pair of short to elongate, denticulate processes.

Panama, Colombia, and Jamaica.

CANAL ZONE: Barro Colorado Island, Wheeler trail, *Shattuck 548;* Upper Chagres River, sea level, *Powell 241;* Cerro Campana, vicinity Campana, 3000 ft., *Allen 5142.* COCLÉ: hills north of El Valle de Antón, 1000 m., *Fairchild s. n.*

Small but attractive epiphytes, vegetatively reminiscent of a slender form of *Brassavola nodosa.* The flowers in the specimens examined are quite variable. In the El Valle and Cerro Campana collections the margins of the lip are conspicuously lacerate while in the lowland specimens they are only minutely denticulate; also, the lateral subulate processes on either side of the clinandrium have been found to be quite variable, scarcely any two specimens being exactly alike. The simpler of these forms very closely approximate the earlier South American *Trichopilia mutica,* and it seems quite probable that a more complete series of collections from the intermediate area would prove the two concepts to be one polymorphic species.

6. TRICHOPILIA TURIALBAE Rchb. f. in Hamb. Gartenzeit. 19:11. 1863, non Batem.

Erect, epiphytic herbs with approximate, linear, strongly ancipitous pseudobulbs 5.5–10 cm. tall and 1.2–1.8 cm. wide, the truncate apices with a single leaf, the bases of the pseudobulbs enveloped in several papery, imbricating bracts. Leaves elliptic-lanceolate, acute, subcoriaceous, 15–20 cm. long and 3.5–5 cm. wide. Inflorescences short, arching or pendulous, 1- to 3-flowered scapes produced from the bases of the pseudobulbs. Flowers of moderate size. Sepals spreading, pure white, 2.5–3 cm. long and 0.4–0.5 cm. wide, the dorsal sepal free, lanceolate, acute, the lateral sepals connate to about the middle, acuminate. Petals subequal to the dorsal sepal, pure white, lanceolate, acuminate, 2.5–3 cm. long and 0.6–0.8 cm. wide. Lip tubular, white with pale orange lines in the throat, obscurely 3-lobed, obovate when spread out, 3.5–4 cm. long and 2.5–3 cm. wide, the narrowed base adnate to the base of the column, the lateral margins convolute and enveloping the column, the mid-lobe retuse at the apex, the lateral lobules reflexed and undulate, the disk with an elongate, central keel exceeding the length of the

column. Column elongate, semiterete, the margins of the apex projecting and forming a distinctly 3-parted, minutely denticulate hood over the anther.

Costa Rica and Panama.

VERAGUAS: mountains of western Azuero, about 600 m., *E. R. Dunn s. n.*

Trichopilia turialbae Rchb. f. is very close to the earlier *T. tortilis*, differing in the smaller size and in color of the flowers, and in the conspicuously connate lateral sepals. However, several Guatemalan collections of *T. tortilis* have been examined in which the flowers closely approximate ours in size. In all the material seen of *T. tortilis*, the lateral sepals were found to be connate at the base in some degree, although none to the middle as in our specimens. It seems rather likely, however, that intermediate forms will eventually be found and that *T. turialbae* will be reduced to varietal status under the archetypal species.

73. MESOSPINIDIUM Rchb. f.

MESOSPINIDIUM Rchb. f. in Bot. Zeit. 10:929. 1852; Walp. Ann. 6:856. 1864.

Epiphytic herbs with slender, complanate, monophyllous pseudobulbs enveloped at the base in several conspicuous, foliaceous bracts. Leaves at the apex of the pseudobulbs and the blades of the foliaceous bracts ligular to elliptic-lanceolate, subcoriaceous to pergameneous, the conduplicate, imbricating bases of the foliaceous bracts forming a 2-ranked, more or less flabelliform cluster. Inflorescences slender, erect or arching panicles or racemes produced from the base of the current pseudobulb. Flowers small, on short, slender pedicels subtended by inconspicuous bracts. Sepals rather fleshy, not widely spreading, the dorsal sepal free, the laterals connate for more than half their length, forming a single bifid segment supporting the lip. Petals oblong, acute to cuneate and aristate, the broad bases inserted on the sides of the column. Lip entire, the base shallowly subsaccate and continuous with the base of the column, the limb oblong, obovate or subpandurate, the margins usually revolute, the apex acute to obtuse and emarginate, the disk with 2 fleshy, converging keels. Column short, very stout, apparently without wings or appendages, the base without a foot; pollinia 2, waxy.

Two or three species of tropical American epiphytes, apparently closely allied to *Oncidium* and *Odontoglossum*. One species is known from Panama.

1. MESOSPINIDIUM WARSCEWICZII Rchb. f. in Bot. Zeit. 10:929. 1852.

Solenidium Endresii Kränzl. in Engl. Pflanzenr. IV, Fam. 50 (Heft 80):317. 1922.

Erect, epiphytic herbs with distichous clusters of foliaceous bracts, the conduplicate bases somewhat enveloping a slender, strongly ancipitous, nearly linear, monophyllous pseudobulb, the plants 12–22 cm. tall. Leaves of the apex of the pseudobulbs and the blades of the foliaceous bracts ligular to elliptic-lanceolate, acute to acuminate, pergameneous, 5–17 cm. long and 1–2.8 cm. wide, contracted below into slender, conduplicate petioles, the persistent bases of the bracts often somewhat broader than the petioles, in dried specimens superficially resembling

the pseudobulbs. Inflorescences 1–2 slender, erect, racemose or paniculate scapes equaling or exceeding the leaves, 12–27 cm. tall, produced from the bases of the pseudobulbs. Flowers small. Sepals rather fleshy, not widely spreading, greenish yellow to tan, often spotted reddish brown, the dorsal sepal ovate, deeply concave, the apex conspicuously aristate, 6–8 mm. long and 2.5–3 mm. wide, the lateral sepals connate for more than half their length, forming a single bifid segment supporting the lip, 6–8 mm. long and 4–5 mm. wide. Petals rather fleshy, oblong-lanceolate, the apices aristate, the broad bases inserted on the sides of the column, the margins scarcely imbricating with those of the sepals, 4–5 mm. long and 2.5–3 mm. wide. Lip fleshy, entire, subpandurate when spread out, 5–7 mm. long and 2.5–3 mm. wide, white to pale yellow, usually with minute red spots, the oblong, subsaccate base continuous with the base of the column, the apex broader, with revolute margins, the disk with 2 converging fleshy keels. Column short, very stout, apparently without wings or appendages, about 4 mm. long and 4 mm. wide, the base without a foot.

Costa Rica and Panama.

PANAMÁ: Cerro Campana, vicinity Campana, in cloud forest near summit, 800–1000 m., *Allen 3966*. COCLÉ: vicinity El Valle de Antón, 650 m., *Fairchild s. n.*; hills north of El Valle de Antón, 1000 m., *Allen 2761, 2785*.

74. ODONTOGLOSSUM HBK.

ODONTOGLOSSUM HBK. Nov. Gen. & Sp. 1:350, *t. 85*. 1816; Benth. & Hook. Gen. Pl. 3:561. 1883.

Cuitlauzina La Llave & Lex. Nov. Veg. Descr. 2:32. 1825.
Cuitlanzina Lindl. Orch. Sel. 15. 1826.
Cuitlauzinia Rchb. Nom. 54. 1841.
Lichterveldia Lem. Illustr. Hortic. 2: *t. 59*. 1855.
Osmoglossum Schltr. in Orchis 10:162. 1916, as subgenus.

Epiphytic herbs with approximate or rarely distant, usually ovoid or elliptic-oblong, compressed, 1- to 3-leaved pseudobulbs, the bases enveloped in a few distichous, papery or foliaceous bracts. Leaves coriaceous or fleshy. Inflorescences produced from the bases of the pseudobulbs, sometimes short and 1-flowered, more frequently elongate, erect or arching, very rarely pendulous, few- to many-flowered racemes or panicles. Flowers usually large and conspicuous, but sometimes small. Sepals subequal, usually spreading, free or rarely with the lateral sepals united. Petals usually subequal to the dorsal sepal but sometimes broader. Lip 3-lobed or entire, the base continuous with the base of the column, the limb erect or parallel with the column, sometimes shortly adnate to it, the lateral lobes (if present) spreading or erect, the mid-lobe usually deflexed, less frequently spreading or concave, the apex acute, obtuse or emarginate, the disk at the base of the lip variously cristate, denticulate, lamellate, or rarely smooth. Column usually longer and more slender than in *Oncidium*, often clavate, the apex without appendages or sometimes with the margins produced into lobes, auricles, or teeth. Anther terminal, operculate, incumbent, 1-celled or imperfectly 2-celled; pollinia 2, waxy.

A large, polymorphic group of highland epiphytes having centers of rich specific and varietal development in the mountains of Mexico and Colombia, with some species ranging as far south as Brazil and Bolivia. As has been pointed out by Dr. Louis Williams in a footnote to the generic key (Ann. Mo. Bot. Gard. 33:7 [Fl. Pan. 3[2]:113]. 1946) the concepts of *Odontoglossum, Miltonia, Mesospinidium, Aspasia, Brassia, Leochilus,* and *Osmoglossum* are technically inseparable from that of the earlier *Oncidium,* and might much more logically be treated as subgeneric sections of that genus. However, the species in each category are generally sufficiently distinctive to be readily recognizable by the average amateur, only the border-line species presenting any great difficulty. Practical ends seem to be better served by the maintainance of these entities as distinct, particularly for a treatment of this type, with the single exception of *Osmoglossum,* which, it appears, was never properly described or published, having been listed by Schlechter merely as a subgenus. Five species have been known from Panama, and a sixth, *Odontoglossum convallarioides,* which is very common in the highlands of adjacent Costa Rica, may possibly be represented in our series of specimens by a single fragmentary collection.

a. Apex of the pseudobulbs monophyllous.
  b. Inflorescences racemose. Plants robust, the pseudobulbs distantly inserted on an elongate rhizome..... 2. O. CHIRIQUENSE
  bb. Inflorescences 1-flowered. Plants dwarf, the pseudobulbs approximate..... 5. O. OERSTEDII
aa. Apex of the pseudobulbs di- or triphyllous.
  b. Inflorescences paniculate..... 1. O. CARINIFERUM
  bb. Inflorescences racemose.
    c. Flowers small, sepals 15 mm. long or less. Leaves narrowly linear.
      d. Lateral sepals connate for more than half their length..... 4. O. ECURTONI
      dd. Lateral sepals not connate..... 3. O. CONVALLARIOIDES
    cc. Flowers large, sepals 30 mm. long or more. Leaves elliptic-lanceolate..... 6. O. SCHLIEPERIANUM

1. ODONTOGLOSSUM CARINIFERUM Rchb. f. in Bot. Zeit. 10:638. 1852.

Oncidium cariniferum (Rchb. f.) Beer, Prakt. Stud. Orch. 283. 1854.
Odontoglossum hastilabium Lindl. var. *fuscatum* Hook. in Bot. Mag. *t. 4919.* 1856.

Large, erect, epiphytic herbs with ovoid to elliptic-oblong, compressed, usually furrowed pseudobulbs 6–12 cm. long and 2.5–8 cm. wide, the apices with 2–3 leaves, the bases partially enveloped in several more or less distichous, imbricating bracts, the upper 2–3 of which are conspicuously foliaceous. Leaves coriaceous, linear-ligular, acute, 30–45 cm. long and 2.5–7 cm. wide. Inflorescences large, stout, erect or arching, many-flowered panicles, conspicuously exceeding the leaves, up to about 1 m. in length. Flowers relatively large, on long, slender pedicels, each subtended by an inconspicuous bract. Sepals subequal, usually free, spreading, brown, usually with yellow tips and margins, lanceolate, acuminate, somewhat concave, with a strongly developed dorsal keel, 2.5–3 cm. long and 0.4–0.6 cm. wide. Petals subequal to the sepals and similarly colored, lanceolate, acuminate, sometimes subfalcately incurving, 2–2.5 cm. long and 0.6–0.8 cm.

wide. Lip inconspicuously 3-lobed, 2–2.2 cm. long and 2–2.2 cm. wide, the much narrower basal half elliptic-oblong, adnate to the base of the column, the narrow lateral margins erect or spreading, the mid-lobe broadly biauriculate, white aging pale yellow, the apex very shortly acute or shallowly emarginate, with a short central apicule, the disk at the base of the lip often stained red, with 2 lateral subfalcate wings, the center with several projecting, fleshy teeth. Column slender, erect, about 10 mm. long, the ventral surface of the lower half conspicuously thickened, with 2 obscure lateral keels, terminating in 2 short, acute, fleshy wings below the stigma.

Costa Rica, Panama, Venezuela, and probably adjacent areas.

CHIRIQUÍ: without definite locality, 4000–5000 ft., *Powell 142*, *Kieswetter s. n.*; vicinity Cerro Punta, headwaters of the Río Chiriquí Viejo, 7000 ft., *Allen 1517*.

A robust species much resembling an Oncidium in vegetative habit, found in our area in Chiriquí Province, at 4000–7000 ft. elevation, where the plants seem to be confined to the tops of the tallest forest trees.

2. ODONTOGLOSSUM CHIRIQUENSE Rchb. f. in Bot. Zeit. 10:692. 1852.

Oncidium chiriquense (Rchb. f.) Beer, Prakt. Stud. Orch. 283. 1854.
Odontoglossum coronarium Lindl. Fol. Orch. Odontog. (21) No. 60. 1852.
Oncidium coronarium (Lindl.) Beer, Prakt. Stud. Orch. 285. 1854.

Robust, epiphytic herbs with stout, elongate, repent or semi-scandent rhizomes, the oblong-ovoid, compressed, monophyllous, usually dull purple pseudobulbs 7–11 cm. long and 4–6 cm. broad, distantly and obliquely inserted on the stems, the bases freely rooting, provided with 2–3 lateral, conspicuously foliaceous bracts, the long internodes completely enveloped in numerous papery, imbricating sheaths. Leaves and the blades of the foliaceous bracts elliptic-oblong, obtuse or retuse, coriaceous, 15–30 cm. long and 6–9 cm. wide, contracted at the base into short, conduplicate petioles. Inflorescences stout, erect, many-flowered racemes 30–45 cm. long. Flowers large and conspicuous, bright yellow richly blotched with reddish brown. Sepals free, subequal, widely spreading, elliptic-oblong to obovate, obtuse, with strongly undulate margins, 2–3 cm. long and 1.6–2 cm. wide. Petals subequal to the sepals and similarly colored, elliptic-oblong to obovate, obtuse to subacute, with strongly undulate margins, 2–3 cm. long and 1.5–1.8 cm. wide. Lip 3-lobed, subpandurate, 1.8–2.5 cm. long, the basal half conspicuously narrower than the apex and shortly adnate to the base of the column, the small lateral lobes erect, rather obliquely auriculate, obtuse, with undulate margins, the mid-lobe broadly spreading or reflexed, obovate, the apex obtuse or emarginate, the disk tuberculate at the base. Column short, stout, somewhat arcuate, 8–10 mm. long, the margins of the apex membranaceous and spreading.

Costa Rica, Panama, Colombia, Peru, and probably adjacent territories.

VERAGUAS: "Wild in Veragua; on the Cordillera of Chiriquí, at the height of 9000 ft., on decayed tree trunks. Flowers in October." *von Warczewicz*.

The type collection of this large-flowered and handsome species was presumably made in Panama, but it has not been found in recent years in our area, although it is fairly well known from adjacent Costa Rica and Colombia. It is often listed in horticultural publications as a variety of *Odontoglossum coronarium*. The reason for such treatment is a bit obscure, since Lindley, on the page following the type description of the latter species (Folia Orchidacea. Odontog. (22) No. 62. 1852), cites the place and date of the prior publication of *O. chiriquense*.

3. ODONTOGLOSSUM CONVALLARIOIDES (Schltr.) Ames & Correll, in Bot. Mus. Leafl. Harv. Univ. 11:19. 1943.

Osmoglossum convallarioides Schltr. in Fedde, Rep. Sp. Nov. Beih. 19:148. 1923.

Slender, erect, epiphytic herbs 30–45 cm. tall, the plants nearly identical with those of *Odontoglossum Egertoni*. Flowers fragrant, white, sometimes tinged with pink or lavender, the disk of the lip usually yellow. Sepals free, subequal, somewhat spreading, elliptic-oblong, acute or subacute, concave, 7–10 mm. long and 3–6 mm. wide. Petals broader than the sepals, obovate to suborbicular, obtuse or minutely apiculate, 6–9 mm. long and 5–7 mm. wide. Lip obscurely 3-lobed, obovate, the apex subacute to obtuse or emarginate, 8–10 mm. long and 6–8 mm. wide, the lateral lobules spreading or semi-erect, the mid-lobe usually concave, the disk with two short keels, produced at the front into 2 erect, incurving, parallel, approximate, denticulate processes, the central area below the base of the column with a low, narrow, cuneate callus. Column short, very stout, about 3 mm. long and 3 mm. wide, the apex with obscure, subentire, membranaceous lobules surrounding the clinandrium, the base without a foot.

Mexico, Guatemala, Honduras, Costa Rica, and probably Panama.

A widespread Central American highland species, very closely allied to *Odontoglossum pulchellum*, but differing in the much smaller flowers, the concave rather than arcuate-deflexed lip, and in the less conspicuous lobules surrounding the clinandrium. Although there are no authentic records to substantiate its occurrence in Panama, one fragmentary collection (*Woodson, Allen & Seibert 875*) looks rather suspiciously like it, and in any event its frequent occurrence in the adjacent Costa Rican highlands would strengthen the probability that it will ultimately be found in Chiriquí.

4. ODONTOGLOSSUM EGERTONI Lindl. in Bot. Reg. n. s. 8: Misc. 50. 1845.

Osmoglossum Egertoni (Lindl.) Schltr. in Orchis 10:166. 1916, in synon.
Osmoglossum acuminatum Schltr. in Fedde, Rep. Sp. Nov. Beih. 17:79. 1922.
Osmoglossum anceps Schltr. loc. cit. 19:147. 1923.

Erect, epiphytic herbs with approximate, narrowly elliptic-oblong or ovoid, tapering, compressed, often ridged, 2- to 3-leaved pseudobulbs 3.5–10 cm. long and 1.5–2.2 cm. wide, the bases partially enveloped in 2–3 distichous, conspicuously foliaceous bracts. Leaves and the blades of the basal bracts usually rather rigidly erect, narrowly linear-ligular, acute or acuminate, coriaceous, 25–45 cm.

long and 0.8–1.5 cm. wide. Inflorescences erect, few-flowered racemes, usually not equaling the leaves, produced from the bases of the pseudobulbs, 20–30 cm. tall, the rachis conspicuously flattened, provided with a few, distant, complanate, conduplicate, acuminate bracts. Flowers small for the genus, white, the disk of the lip yellow with reddish spots. Sepals not widely spreading, lanceolate to elliptic-lanceolate, acute to shortly acuminate, concave, the dorsal sepal free, 1.2–1.5 cm. long and 0.4–0.6 cm. wide, the laterals united to beyond the middle, forming a single bifid segment below the lip, 1.3–1.5 cm. long and 0.6–0.8 cm. wide. Petals rather oblique, subequal to the dorsal sepal, ovate-elliptic, acute or shortly acuminate, 1–1.3 cm. long and 0.5–0.8 cm. wide. Lip entire, elliptic-oblong, acute or shortly acuminate, 10–12 mm. long and 6–7 mm. wide, somewhat concave or spreading, the apex sometimes reflexed, the disk with two low keels converging at the front and produced into 2 erect, parallel, fleshy teeth, the central area below the base of the column with a low, narrow, cuneate callus. Column very short, stout, 2–3 mm. long and 2–3 mm. wide, the apex with short, membranaceous, 3-parted, fimbriate to denticulate projections surrounding the clinandrium.

Mexico, Guatemala, Honduras, Costa Rica, and Panama.

CHIRIQUÍ: without definite locality, 6000 ft., *Powell 255*.

Our specimens have somewhat narrower sepals and petals, and a somewhat more acuminate lip than in the type, but otherwise do not differ in the presence or absence of any essential character. It seems possible that all of the species of this alliance will ultimately be reduced to sub-specific rank or synonymy under the two distinctive archetypes, *O. pulchellum* and *O. Egertoni*.

5. ODONTOGLOSSUM OERSTEDII Rchb. f. in Bonplandia 3:214. 1855.

Dwarf, erect, epiphytic herbs up to 22 cm. tall, with approximate, ovoid, usually somewhat compressed, monophyllous pseudobulbs 1–3 cm. long and 0.8–1.8 cm. wide, the bases enveloped in several thin, papery, imbricating, non-foliaceous bracts which soon weather away. Leaves linear-ligular to elliptic-lanceolate, acute, coriaceous, 5–18 cm. long and 0.8–3 cm. wide, contracted below into elongate, slender, conduplicate petioles. Inflorescences erect, slender, 1-flowered scapes equaling or exceeding the leaves, 5–15 cm. long, produced from the bases of the pseudobulbs. Flowers of moderate size, solitary, white, fragrant, the base of the lip with a golden-yellow blotch, the callus densely spotted orange. Sepals free, subequal, spreading, elliptic-oblong, obtuse to subacute, sometimes with a short apicule, 12–20 mm. long and 6–10 mm. wide. Petals subequal to the sepals or sometimes broader, oblong-obovate to elliptic-oblong, obtuse, 12–20 mm. long and 8–12 mm. wide. Lip obovate, shortly clawed at the base, the narrow claw adnate to the base of the column, the apex of the lip broadly spreading, deeply emarginate and 2-lobed, 1.5–2.5 cm. long and 1.5–2.5 cm. wide, the disk with a short, erect, subquadrate, bicarinate, fleshy callus, the center concave, the posterior margin

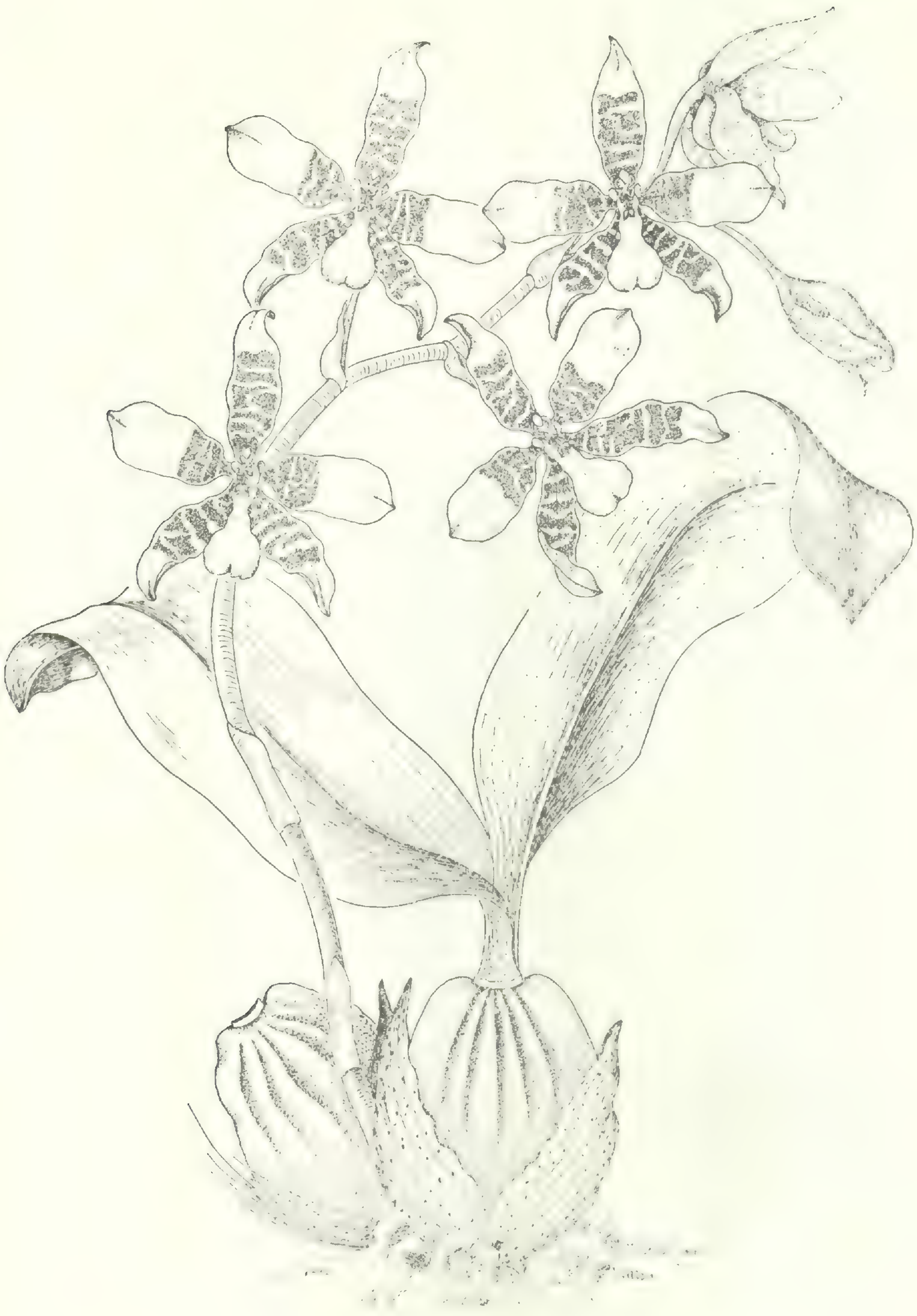


Fig. 192. *Odontoglossum Schlieperianum*

directly below the column minutely ciliate. Column short, stout, 5–7 mm. long, without wings or appendages, the base without a foot.

Costa Rica and Panama.

CHIRIQUÍ: Potrero Muleto to the summit of Chiriquí Volcano, 3500–4000 m., *Woodson & Schery 455;* Loma Larga to the summit, 2500–3380 m., *Woodson, Allen & Seibert 1030;* Casita Alta to Cerro Copete, 2300–3300 m., *Woodson & Schery 337;* without definite locality, 10,000 ft., *Davidson 1001;* summit of Cerro Copete, on dead branches in Ericaceous barrens, 9000 ft., *Allen 4905.*

A small but attractive species rather frequent on the highest slopes of Chiriquí Volcano at 7,000–10,000 ft. elevation. Descriptions in horticultural publications usually indicate that the scapes are 2- to 5-flowered, yet none of the fairly extensive series of specimens in the Ames Herbarium show this to be the case, all having solitary flowers, which has also been the writer's observation in the field in the Chiriquí highlands and in Costa Rica. It seems possible that the plant illustrated in the 'Botanical Magazine' (*t. 6820*) under the name of *Odontoglossum Oerstedii* may be a white-flowered form of *O. Krameri.*

6. ODONTOGLOSSUM SCHLIEPERIANUM Rchb. f. in Gard. Chron. 1082. 1865.

Odontoglossum Insleayi Bark. var. *macranthum* Lindl. Fol. Orch. Odontog. (4). 1852.
Odontoglossum Warscewiczii Bridges ex Stein, Orchideenb. 398. 1892.
Odontoglossum Powellii Schltr. in Fedde, Rep. Sp. Nov. Beih. 17:78. 1922.
Odontoglossum grande Lindl. var. *pallidum* Hort. ex. Sanders, Orchid Guide 313. 1927.

Erect, epiphytic or sometimes pseudoterrestrial herbs with approximate, fleshy, elliptic-oblong or ovoid, compressed, centrally ridged, grayish green, diphyllous pseudobulbs 4–12 cm. long and 2.5–5.5 cm. wide, the bases enveloped in several thin, papery, imbricating bracts which soon weather away. Leaves lanceolate to elliptic-lanceolate, acute, subcoriaceous, 10–30 cm. long and 3–7 cm. wide, contracted below into short or elongate, conduplicate petioles. Inflorescences stout, erect, 2- to 8-flowered racemes equaling or exceeding the leaves, 18–35 cm. long, produced from the bases of the pseudobulbs. Flowers large, yellow or greenish yellow, conspicuously barred and blotched with reddish brown. Sepals subequal, free, spreading, lanceolate, acuminate, 3–4.5 cm. long and 1–1.5 cm. wide. Petals broader than the sepals, oblong-oblanceolate, obtuse to subacute, 3–3.5 cm. long and 1.5–2 cm. wide. Lip obscurely 3-lobed, subpandurate when spread out, 2–3 cm. long and 1.0–1.5 cm. wide, the base contracted into a narrow claw which is adnate to the base of the column, the lateral lobes small, rounded or suborbicular, erect in natural position, the mid-lobe spatulate to obovate, obtuse or retuse, about ¾ the total length of the lip, the disk with a short, central keel, from the mid-section and apex of which are produced 2 pairs of short, spreading, fleshy auricles. Column short, about 10 mm. long, terete below, dilated above, with a slender, acuminate, incurving tooth on each side of the stigma.

Costa Rica and Panama.

CHIRIQUÍ: vicinity Casita Alta, Finca Lérida, eastern slopes of Chiriquí Volcano, 1500–2000 m., *Woodson, Allen & Seibert 790;* vicinity Boquete, 3800–5500 ft., *Pring s. n., Davidson 797;* without definite locality, "In gulch, in damp shady places," 3800 ft., *Powell 178;* valley of the upper Río Chiriquí Viejo, 1300–1900 m., *Seibert 227;* vicinity Paso Ancho, Bambito Woods, along Río Chiriquí Viejo, 4500–5000 ft., *Allen 54.*

A common species of the Chiriquí highlands, closely allied to *Odontoglossum grande* of Mexico and Guatemala.

75. ASPASIA Lindley

ASPASIA Lindl. Gen. & Spec. Orch. Pl. 139. 1833; Benth. & Hook. Gen. Pl. 3:560. 1883.

Trophianthus Scheidw. in Otto & Dietr. Allg. Gartenzeit. 12:218. 1844.

Epiphytic herbs with short, erect, approximate, usually complanate, cylindric stems conspicuously thickened above into compressed, 1- to 2-leaved pseudobulbs, the lower stems and bases of the pseudobulbs invested by the conduplicate, distichously imbricating bases of several conspicuous, foliaceous bracts. Leaves and bract blades coriaceous or subcoriaceous. Inflorescences 1–2 short, erect, few-flowered racemes or rarely 1-flowered scapes, not equaling the leaves, produced from the axils of the uppermost foliaceous bracts. Flowers relatively large to small. Sepals of about equal length, spreading, the dorsal sepal subequal to the petals, the bases of the 3 upper segments connivent and adnate to the column usually somewhat above the insertion of the free lateral sepals. Lip shortly and narrowly clawed at the base, the claw adnate to the lower half of the column, the free limb spreading or with the apical half somewhat porrect, obscurely 3-lobed, subpandurate, subquadrate, suborbicular or obovate, sometimes entire, the lateral lobes (if present) rather broad, subdistinct or confluent with the usually larger mid-lobe. Column erect, semiterete, sometimes somewhat arcuate, the lower half connate with the claw of the lip, the ventral surface below the stigma broadly or narrowly sulcate, the margins sometimes with 2 short, denticulate projections, the apex truncate or sometimes continued into a short membranaceous hood over the anther, the column otherwise wingless, the base without a foot. Anther terminal, operculate, incumbent, 2-celled; pollinia 2, waxy.

About ten species of tropical American epiphytes, ranging from Guatemala to Brazil. Two of these and one variety are thus far known from Panama.

a. Pseudobulbs monophyllous. Plants 25 cm. tall or less. Column less than 6 mm. long ..... 3. A. PUSILLA
aa. Pseudobulbs diphyllous. Plants more than 25 cm. tall. Column 1.5 cm. long or more.
  b. Lateral sepals 1.5–2.2 cm. long, with broad transverse markings. Column with an elliptic depression below the stigma. Apical half of the lip porrect ..... 1. A. EPIDENDROIDES
  bb. Lateral sepals 2.5 cm. long or more, with narrow longitudinal stripes. Column with a narrow linear groove below the stigma. Apical half of the lip not porrect ..... 2. A. EPIDENDROIDES var. PRINCIPISSA

Fig. 193. *Aspasia epidendroides*

1. ASPASIA EPIDENDROIDES Lindl. in Hook. Jour. Bot. 1:6. 1834.

Aspasia fragrans Kl. Ind. Sem. Hort. Bot. Berol. 12. 1852.
Odontoglossum Aspasia Rchb. f. in Walp. Ann. 6:851. 1861.

Erect, epiphytic herbs with linear to oblong-elliptic, laterally compressed, diphyllous, stipitate pseudobulbs 5–14 cm. long and 2–6 cm. wide, the more robust plants having one side of the pseudobulb flattened, while the other surface is conspicuously convex, the complanate-cylindric lower portions and bases of the pseudobulbs invested with several closely imbricating bracts, the uppermost 2–3 of which are distichously arranged and conspicuously foliaceous. Leaves lanceolate to ligular, acute, subcoriaceous, 10–28 cm. long and 1.5–5 cm. wide. Inflorescences 1–2 simple, erect, few-flowered racemes 9–25 cm. long. Flowers of moderate size, the sepals greenish with broad transverse bands of brown or brownish lavender, the petals pale lavender to greenish brown, the lip white, with conspicuous purple or lavender markings in the center, the disk yellow, the column and anther tinged with lavender. Sepals of about equal length, elliptic-obovate, shortly acute, the apex concave with a short fleshy apiculate keel or thickening on the dorsal surface, 1.3–2 cm. long and 0.7–1.0 cm. wide, the base adnate to the base of the column slightly above the insertion of the petals, the lateral sepals strongly reflexed, narrowly and somewhat obliquely oblanceolate, acute, 1.5–2.2 cm. long and 0.6–0.8 cm. wide, the dorsal surfaces thickened into short apiculate keels at the apices. Petals subequal to the dorsal sepal, elliptic-obovate, concave, 1.5–1.8 cm. long and 0.6–0.9 cm. wide, the apices thickened into short, acute keels on the dorsal surfaces. Lip clawed at the base, the claw adnate to the lower half of the column, the free limb abruptly deflexed, obscurely 3-lobed, subquadrate, 1.2–1.6 cm. long and 1.4–1.8 cm. wide, the basal and apical halves of about equal width, the lateral margins at the base spreading, the mid-lobe emarginate and 2-lobed, with a thickened central keel, usually more or less porrect, the disk with 2 narrow parallel keels about equaling the lateral lobes of the lip in length. Column semiterete, slightly arcuate, about 1.5 cm. long, with a narrowly elliptic concavity below the stigma.

Guatemala, Honduras, Nicaragua, Costa Rica, and Panama.

PANAMÁ: along road to Pacora, about 50 m., *Allen 822.* COCLÉ: mountains beyond La Pintada, 400–600 m., *Hunter & Allen 633;* Penonomé and vicinity, 50–1000 ft., *R. S. Williams 445.* VERAGUAS: vicinity Santiago, 600–800 ft., *Powell 3542;* vicinity Río de Jesús, sea level, *Allen & Allen 4273.* CHIRIQUÍ: without definite locality, *Powell 3017.*

2. ASPASIA EPIDENDROIDES var. PRINCIPISSA (Rchb. f.) P. H. Allen, stat. nov.

Aspasia principissa Rchb. f. in Bot. Zeit. 10:367. 1852.
Aspasia Rousseauae Schltr. in Gartenfl. 71:76. 1922.

Epiphytic herbs often nearly identical to *Aspasia epidendroides*, but usually somewhat less robust and with larger flowers. Sepals subequal, spreading, lanceolate, acute to acuminate, pale green, longitudinally striped brown, the apices thickened and somewhat concave, usually 2.5–3 cm. long and 0.5–0.7 cm. wide,

Fig. 194. *Aspasia epidendroides* var. *principissa*

the dorsal sepal connivent at the base with the bases of the petals and adnate to the column somewhat above the insertion of the lateral sepals. Petals a little broader than the sepals, spreading, lanceolate, acute, 2.2–2.8 cm. long and 0.6–0.9 cm. wide. Lip narrowly clawed at the base, the claw adnate to the lower half of the column, the free limb abruptly deflexed, explanate, obscurely 3-lobed, subpandurate, 2–3 cm. long and 1.8–2.6 cm. wide, the basal half usually conspicuously broader than the apical half, the lateral lobes rounded and spreading, the mid-lobe emarginate, the lateral lobules somewhat undulate but never porrect, the disk with numerous radiating thickened nerves, the central 2 of

which are parallel and exceeding the others, about equaling the lateral lobes of the lip in length. Column semiterete, lightly arcuate, 1.8–2 cm. long, creamy white aging pale yellow, adnate to the claw of the lip for about half of its length, the ventral surface below the stigma with a narrow groove, the base of the column without a foot.

Costa Rica and Panama.

CANAL ZONE: wet forest bordering Gatún Lake, 30 m., *Killip 3447;* Culebra, 50–100 m., *Pittier 3396;* Cruces, sea level, *Powell 3108.* PANAMÁ: foothills near Panama City, sea level, *Powell 39;* Juan Díaz, sea level, *Powell 3038;* Chiva-Chiva, sea level, *Powell 3029;* Río La Maestra, Pacific coast between the Río Bayano and the Gulf of San Miguel, 0–25 m., *Allen 68;* San Jose Island, Perlas Archipelago, *Johnston 136, 702, 1015, 1288, Erlanson 199.* COLÓN: Quebrada Salamanca, upper Madden Lake region, 70 m., *Dodge, Steyermark & Allen 16990;* forests along the Río Boquerón, above the Peluca Hydrographic Station, 90 m., *Hunter & Allen 653;* Río Viejo, vicinity Puerto Pilón, sea level, *Allen 4252.* DARIÉN: forests around Yaviza, *Pittier 6581;* vicinity Marragantí, 10–200 ft., *R. S. Williams 969.*

An attractive, large-flowered variety of *Aspasia epidendroides,* usually confined to areas of higher rainfall, being known from the vicinity of Puerto Limón, on the Atlantic coast of Costa Rica, and ranging eastward along the Atlantic seaboard, probably as far as Colombia. In the Canal Zone area, it follows the Río Chagres drainage to the headwaters of Madden Lake, crossing to the Pacific slope in the forested hills east of Panama City and continuing into Darién Province and the Perlas Islands, replacing the typical form from the Canal area eastward.

3. ASPASIA PUSILLA C. Schweinf. in Bot. Mus. Leafl. Harv. Univ. 10:21, *t. 1.* 1941.

Small, erect, epiphytic herbs with approximate, linear or ellipsoid-complanate, monophyllous pseudobulbs 2.5–4 cm. long and 1.0–1.5 cm. wide, the complanate-cylindric, stipitate bases invested by several distichously imbricating, conduplicate sheaths the upper 2–3 of which are conspicuously foliaceous and enveloping the lower portions of the pseudobulbs. Leaves linear-ligular, obliquely acute, subcoriaceous, up to 17 cm. long and 1.5 cm. wide, contracted below into short conduplicate petioles. Inflorescences slender, erect, few-flowered racemes up to about 8 cm. long. Flowers small for the genus, on long slender pedicels, the sepals and petals yellow to greenish yellow with a dark brown basal blotch, the lip white or pale yellow, the disk orange marked with mauve or maroon stripes. Sepals subequal, free, spreading, the dorsal sepal elliptic-lanceolate to oblanceolate, acute, about 13 mm. long and 4.5 mm. wide, the laterals lanceolate, acute, about 13.5 mm. long and 4 mm. wide. Petals subequal to the dorsal sepal, elliptic-oblanceolate, obliquely acute, about 12 mm. long and 4 mm. wide. Lip clawed at the base, the claw adnate to the lower half of the column, the free limb suborbicular to obovate, entire, about 11 mm. long and 12 mm. wide, the apex slightly retuse, broadly spreading, the base somewhat concave, the disk with a short pubescent, divaricate callus. Column very short, stout, about 5.5 mm. long, the apex with a denticulate

Fig. 195. *Aspasia pusilla*

hood over the anther, the lateral margins below the stigma with 2 short, porrect, obliquely triangular teeth.

Costa Rica and Panama.

DARIÉN: Cana-Cuasi trail, hills near Chepigana, 2000 ft., *Terry & Terry 1502.*

A very distinctive dwarf species, known in our area only from the type collection.

76. BRASSIA R. Brown

BRASSIA R. Br. in Ait. Hort. Kew. 2:215. 1813; Benth. & Hook. Gen. Pl. 3:564. 1883.

Erect, epiphytic herbs with short stems usually thickened into conspicuous pseudobulbs that are infrequently rudimentary and inconspicuous or rarely entirely absent, the 1–3 leaves at the apex enveloped in several foliaceous or papery bracts, the conduplicate leaf bases distichously imbricating and forming a broad or narrow fan. Inflorescences 1–2 erect or arching, few- to many-flowered racemes produced from the bases of the pseudobulbs or concurrently with the flush of new growth, or, if the plants are pseudobulbless, from the axils of the leaves. Flowers usually large and conspicuous, subtended by small and inconspicuous, or elongate spathaceous bracts. Sepals free, spreading, narrowly acuminate or caudate, sometimes of about equal length but more frequently with the lateral sepals conspicuously longer. Petals subequal to the dorsal sepal or smaller. Lip entire or obscurely 3-lobed, spreading, shorter than the sepals, the base sessile and adnate to the base of the column, the disk usually bilamellate. Column short, erect, without wings or appendages, the clinandrium scarcely prominent, usually truncate. Anther terminal, operculate, incumbent, 1-celled or imperfectly 2-celled; pollinia 2, waxy.

A small genus of American epiphytes, ranging from southern Florida and the West Indies to Mexico, Central America, and northern South America to Brazil, Bolivia, and Peru. They are technically inseparable from *Oncidium*, yet the majority of the species can readily be distinguished by the conspicuously elongate lateral sepals. Five species are known from Panama.

a. Plants without pseudobulbs, or apparently so.
  b. Leaves many, forming a broad fan, entirely without pseudobulbs. Lateral sepals 3.5 cm. long or more ..... 1. B. ALLENII
  bb. Leaves few, forming a narrow distichous petiole, usually enveloping a small rudimentary pseudobulb. Lateral sepals 2 cm. long or less .... 3. B. CHLOROPS
aa. Plants without conspicuous pseudobulbs.
  b. Lateral sepals 2 cm. long or less ..... 3. B. CHLOROPS
  bb. Lateral sepals 3 cm. long or more.
    c. Pseudobulbs monophyllous at the apex ..... 5. B. LONGISSIMA
    cc. Pseudobulbs diphyllous or rarely triphyllous at the apex.
      d. Apical half of the lip conspicuously broader than the basal half. Calli thickened into broad plates at the front. Highland species ..... 4. B. GIREOUDIANA
      dd. Apical half of the lip not conspicuously broader than the basal half. Calli at the front with 2 separate and distinct slender teeth. Lowland species ..... 2. B. CAUDATA

1. Brassia Allenii L. O. Wms. ex C. Schweinf. in Bot. Mus. Leafl. Harv. Univ. 13:145, *t. 12.* 1948.

Erect, epiphytic herbs entirely without pseudobulbs, the plants 30–38 cm. tall, nearly identical in vegetative appearance with *Huntleya meleagris*. Leaves 8–14, distichously arranged in the form of a broad fan, linear-ligular to lanceolate, usually shortly and subfalcately acuminate, subcoriaceous, 15–35 cm. long and 2–4 cm. wide, the conduplicate bases 2-ranked and closely imbricating, usually slightly broader at the suture line than the leaf petioles. Inflorescences erect or arching, 5- to 8-flowered, congested racemes ½ to ⅔ the length of the leaves. Flowers of moderate size, the lip usually uppermost in natural position, very fragrant, subtended by broad, acute or acuminate, papery, spathaceous bracts. Sepals subequal, free, spreading, reddish tan to olive-ocher, shading to cinnamon-buff at the base, linear-lanceolate, long-acuminate, 3.5–4 cm. long and 0.4–0.5 cm. wide. Petals subequal to the sepals and similarly colored, with a small triangular barium-yellow spot at the base, obliquely lanceolate, long-acuminate, the attenuate apices subfalcately incurving, 3–4 cm. long and 0.5–0.6 cm. wide. Lip entire, subquadrate to suborbicular, spreading, slightly convex, 15–20 mm. long and 13–16 mm. wide, barium-yellow, with a narrow, semicircular band of Mikado brown spots surrounding the disk, the base sessile and adnate to the base of the column, the apex abruptly contracted into an elongate, acuminate apicule, the disk white, with 2 short, stout, erect, parallel, strontian yellow keels, terminating at the front in 2 short, obtuse, subconic teeth. Column very short, stout, terete, about 5 mm. long, green or white, with 2 lateral Mikado brown blotches, without wings or appendages, the base without a foot.

Panama.

Panamá: cloud forest on summit of Cerro Campana, 3000 ft., *Allen & Fairchild 5150.* Coclé: mountains beyond La Pintada, 400–600 m., *Hunter & Allen 592;* hills north of El Valle de Antón, 800–1000 m., *Fairchild s. n., Ohlson s. n., Allen 374, 2830, 2922, 3717.*

A very distinctive species entirely without pseudobulbs, apparently most nearly allied to *Brassia glumacea* Lindl. of Venezuela. The plants are nearly identical in superficial appearance with those of *Huntleya meleagris*, sometimes differing in the shortly and subfalcately acuminate apices of the leaves, and in the conduplicate leaf bases which are often rather noticeably dilated at the suture line and not uninterruptedly confluent with the leaf petioles, as in the latter. All specimens seen have originated in the cool wet forests north of El Valle de Antón, the cloud forest cap of Cerro Campana, or in the mountains west of Santa Fé, in Veraguas; the only presently accessible areas in Panama representative of the extensive and poorly known intermediate highlands of the Atlantic slope.

2. Brassia caudata (L.) Lindl. in Bot. Reg. 10: *t. 832.* 1824.

Epidendrum caudatum L. Sp. Pl. ed 2, 1349. 1763.
Malaxis caudata Willd. Sp. Pl. 4:93. 1805.
Oncidium caudatum Rchb. f. in Walp. Ann. 6:766. 1863.

Fig. 196. *Brassia Allenii*

Brassia Lewisii Rolfe, in Orch. Rev. 1:199. 1893.
Brassia longissima (Rchb. f.) Schltr. var. *minor* Schltr. in Fedde Rep. Sp. Nov. Beih. 17:80. 1922.

Fig. 197. *Brassia caudata*

Erect, epiphytic herbs with approximate, linear to oblong-elliptic, ancipitous pseudobulbs 6–15 cm. long and 2–4 cm. wide, the truncate apices usually with 2 or rarely with 3 leaves, the bases of the pseudobulbs enveloped in 4–6 papery, closely imbricating bracts, the uppermost sometimes foliaceous. Leaves ligular to elliptic-oblong, obtuse to shortly acute, coriaceous, 16–27 cm. long and 2.5–6 cm. wide, contracted below into short conduplicate petioles. Inflorescences 1 or 2 arching, unbranched, usually 6- to 12-flowered racemes 15–30 cm. long, produced from the lateral bases of the pseudobulbs, the rachis often dull red, often rather complanate. Flowers large, with conspicuous caudate lateral sepals. Sepals free, spreading, greenish yellow to yellow, usually spotted reddish brown, particularly near the base, the dorsal sepal erect, linear-lanceolate, long-attenuate, 4–9 cm. long and 0.4–0.7 cm. wide, the apical half usually incurving, the lateral sepals conspicuously longer, caudate, of quite variable length, 12–30 cm. long and 0.5–0.6 cm. wide at the base, the outer surfaces with a strongly developed central keel. Petals free, greenish yellow or yellow, usually heavily spotted reddish brown near the base, the long attenuate apices falcately incurving, 2–3 cm. long and 0.3–0.4 cm. wide. Lip entire, oblong-lanceolate, long-acuminate, somewhat convex, often with deflexed lateral margins, yellow with reddish brown markings at the base, 3–5 cm. long and 1.0–1.2 cm. wide, the base sessile and adnate to the base of the column, the disk with 2 erect parallel lamellae in front of which are 2 short, distinct, acute teeth. Column stout, 4–5 mm. long, without wings or appendages, the base without a foot.

Mexico to Brazil and Bolivia; Florida; Greater Antilles.

CANAL ZONE: Miraflores, *Powell 3231;* Frijoles, *Powell 3117, 3256, Killip 3448;* Pedro Miguel, *Powell 3258, 3530, 3566;* Ancón, *Pittier 6631;* Barro Colorado Island, Gatún Lake, *Shattuck 202.* PANAMÁ: hills east of Panama City, *Powell 3275, Allen 4560.* DARIÉN: vicinity La Palma, 0–50 m., *Pittier 6619.* CHIRIQUÍ: exact locality lacking, sea level, *Powell 87.*

A very common and widely distributed species of the lowlands of the American tropics and subtropics. The flowers are somewhat variable in size, those with the longest sepals sometimes being confused with *Brassia longissima,* a very different species with monophyllous pseudobulbs, of the cool intermediate highland forests of the Atlantic slope. *Brassia longissima* var. *minor* is simply a small-flowered form of *B. caudata.*

3. BRASSIA CHLOROPS Endres & Rchb. f. in Gard. Chron. 542. 1873.

Brassia parviflora A. & S. in Sched. Orch. 8:74. 1925.

Erect, caespitose, epiphytic herbs usually with slender, complanate-elliptic, rudimentary, monophyllous pseudobulbs often completely enveloped by the conduplicate leaf bases. Leaves lanceolate, shortly acuminate, subcoriaceous, 8–30 cm. long and 1.4–3.0 cm. wide, the conduplicate bases distichously imbricating, often forming a short, narrow, complanate petiole, the leaves toward the base becoming progressively shorter, the lowest reduced to non-foliaceous bracts. In-

florescences erect, 3- to 7-flowered racemes 15–25 cm. long, produced from the axils of the upper leaves. Flowers very small for the genus. Sepals rather fleshy, free, subequal, spreading, linear-lanceolate, acuminate, 1.4–2 cm. long and 0.2–0.3 cm. wide. Petals subequal to the dorsal sepal, obliquely lanceolate, acuminate, 1.1–1.5 cm. long and 0.15–0.25 cm. wide. Lip entire, rather fleshy, elliptic-lanceolate to linear-lanceolate, acute, 1–1.1 cm. long and about 0.45 cm. wide, the apex usually dorsally carinate and recurved, the base adnate to the base of the column, the disk with 2 fleshy parallel pubescent keels, about ½ the total length of the lip, the apices terminating in 2 more or less prominent teeth. Column short, stout, about 5 mm. long, the base without a foot.

Costa Rica and Panama.

CHIRIQUÍ: vicinity Casita Alta, Finca Lérida, eastern slopes of Chiriquí Volcano, 1500–2000 m., *Woodson, Allen & Seibert 874.*

An aberrant highland species, having the aspect of a small-flowered *Odontoglossum*. It differs from most species of *Brassia* in the short sepals which are of about equal length, green with darker spots or brown with yellow markings. Our single specimen differs in color, and somewhat in structural detail from the type, but seems more readily referable to this species than to any other.

4. BRASSIA GIREOUDIANA Rchb. f. & Warscz. in Otto & Dietr. Allg. Gartenzeit. 22:273. 1854.

Oncidium Gireoudianum Rchb. f. in Walp. Ann. 6:768. 1863.

Erect, epiphytic herbs with approximate, fleshy, elliptic-ovoid, rather compressed, usually longitudinally ridged, diphyllous pseudobulbs 7–11 cm. long and 2.5–4 cm. wide, the bases enveloped in several papery, imbricating bracts the uppermost 1–2 of which are sometimes foliaceous. Leaves ligular to lanceolate, acute, coriaceous, 22–35 cm. long and 2–5 cm. wide, the bases contracted into short conduplicate petioles. Inflorescences usually solitary, elongate, arching, many-flowered racemes equaling or exceeding the leaves, usually produced concurrently with the flush of new growth from the axils of the expanding leaves or sometimes from the bases of the newly completed pseudobulbs. Flowers large and conspicuous, with elongate filiform sepals and petals. Sepals free, widely spreading, long-attenuate, greenish yellow with a few brown blotches near the base, the dorsal sepal narrowly linear-lanceolate, 9–10 cm. long and 0.3–0.4 cm. wide near the base, the lateral sepals somewhat longer, narrowly linear-lanceolate, 10–15 cm. long and 0.4–0.5 cm. wide near the base. Petals subequal to the dorsal sepal, spreading, the apical half greenish yellow, the basal half brown, narrowly linear-lanceolate, long-attenuate, 5–6 mm. long and 3–4 mm. wide near the base. Lip entire, rather rhombic in outline, 3–4.5 cm. long and 1.5–2.5 cm. wide, pale yellow with sparse brown spots and blotches, the basal portion subquadrate to oblong, adnate to the base of the column, the apical portion abruptly dilated and cordate, shortly acuminate or apiculate, the disk with 2 fleshy, minutely puberulent

keels, the basal portions erect and parallel, terminating at the apex in 2 larger subquadrate spreading lobules. Column very short, stout, 3.5–5 mm. long, the base without a foot.

Costa Rica and Panama.

CHIRIQUÍ: "On banks of rivers", 3500–4500 ft., *Powell 143;* Llano del Volcán, and along Río Chiriquí Viejo, 1200 m., *Allen 915.*

5. BRASSIA LONGISSIMA (Rchb. f.) Nash in Bailey, Stand. Cyclop. Hort. 1:541. March, 1914.

Brassia Lawrenciana Lindl. var. *longissima* Rchb. f. in Gard. Chron. 1313. 1868.
Brassia longissima (Rchb. f.) Schltr. Die Orchideen, 496. October 1914, as to basinym, but only in part as to plant described.

Erect, epiphytic herbs with approximate, very strongly flattened, oblong to elliptic-oblong, monophyllous pseudobulbs, with very thin, acute margins, 4–16 cm. long and 3–5 cm. wide, the bases enveloped in several conduplicate, imbricating, papery bracts, the uppermost one of which is usually shortly foliaceous. Leaves oblong-lanceolate, acute, coriaceous, 25–55 cm. long and 4–7 cm. wide, the bases contracted into very short, conduplicate petioles. Inflorescences 1 or rarely 2, arching, few-to many-flowered racemes 25–45 cm. long, produced from the bases of the pseudobulbs. Flowers large and conspicuous, with elongate, filiform, lateral sepals. Sepals yellow to greenish yellow, spotted or blotched reddish brown near the base, the dorsal sepal narrowly linear-lanceolate, long-attenuate, 8–10 mm. long and 3–4 mm. wide at the base, the lateral sepals conspicuously longer, narrowly linear-lanceolate, caudate, 10–18 cm. long and 0.3–0.4 cm. wide. Petals shorter than the dorsal sepal, yellow to greenish yellow, reddish brown near the base, narrowly linear-lanceolate, the attenuate apices subfalcately incurving, 4–5 cm. long and 0.3–0.4 cm. wide at the base. Lip entire, pale yellow to greenish white, with sparse reddish brown spots near the base, lanceolate, acuminate, 3–5 cm. long and 1.0–1.5 cm. wide, the base somewhat concave with erect margins, adnate to the base of the column, the disk with an erect, fleshy, minutely puberulent, bilamellate, obliquely truncate callus. Column short, semiterete, about 8 mm. long, the base without a foot.

Costa Rica, Panama, Peru, and probably adjacent territories.

COCLÉ: region north of El Valle de Antón, 1000 m., *Fairchild s. n.;* Loma del Tigre, hills north of El Valle, 3000 ft., *Allen 4562.*

This very distinctive species has thus far been found only twice in Panama, both times in the wet highland forests north of El Valle de Antón, in Coclé Province, at about 3000 ft. elevation, although the species is to be expected generally in similar areas on the Atlantic slope.

Since there seems to be some confusion in regard to the application of the name *Brassia longissima,* it might be well to give something of its history. Both

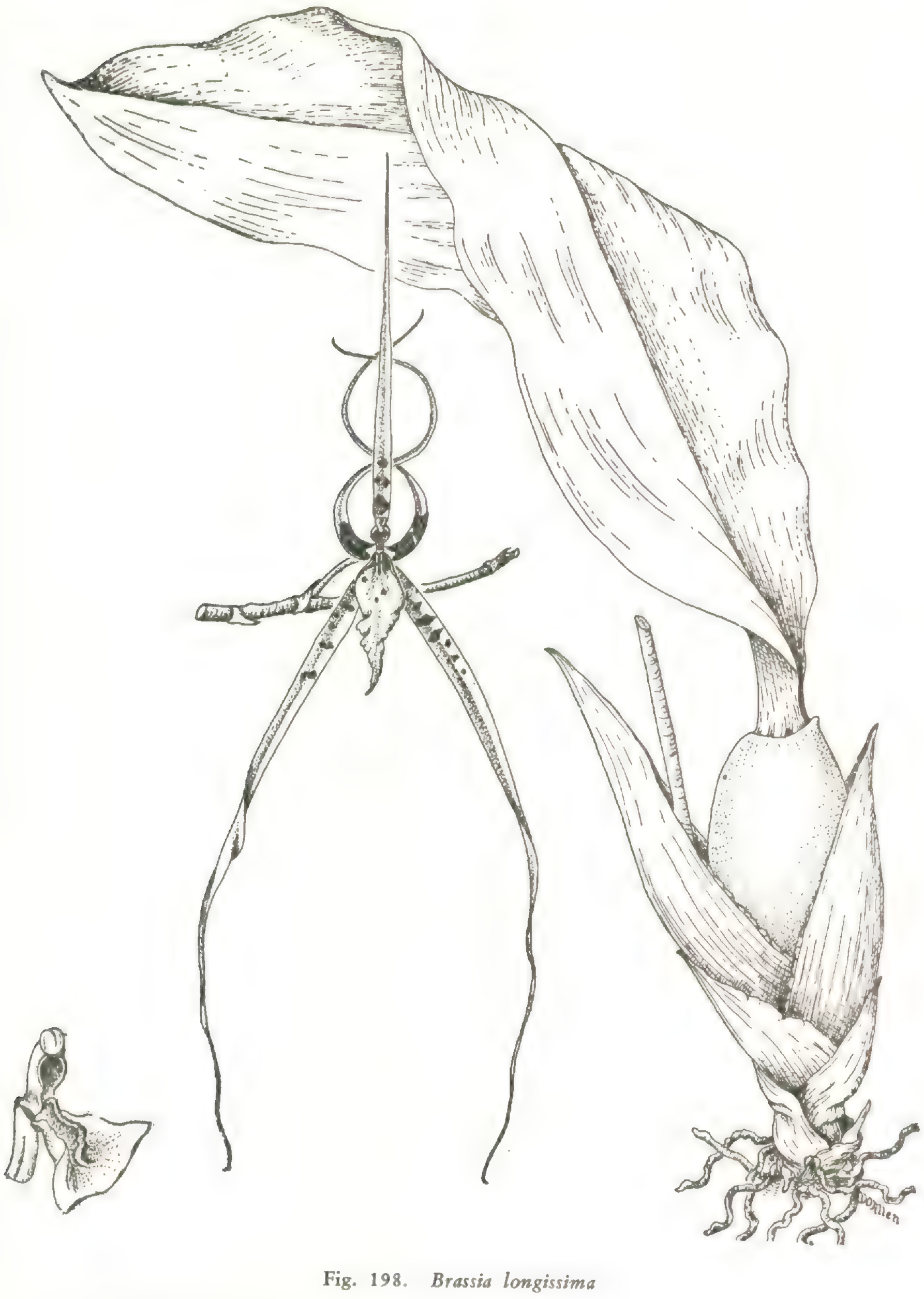


Fig. 198. *Brassia longissima*

Nash (in Bailey Stand. Cyclop. Hort. 1:541. March, 1914) and Schlechter (Die Orchideen, 496. October, 1914) decided that the entity hitherto known as *Brassia Lawrenciana* Lindl. var. *longissima* Rchb. f. actually represented a distinct species, citing Reichenbach's variety as the name-bringing synonym. The

accompanying description given by Nash, whose publication antedated that of Schlechter by some six months, essentially followed Reichenbach's original, while that of Schlechter was apparently based on two distinct elements: the Reichenbach variety of *B. Lawrenciana*, and a very different plant that we now know was a large-flowered form of *B. caudata* (*Powell 87*). Although under the rules, the name of *B. longissima* (Rchb. f.) Schltr. must be regarded as synonymous with the name-bringing synonym, or the first published derivative name therefrom, there can be no doubt that the plant which Schlechter had in mind was a large-flowered form of *B. caudata*. This is further borne out by his subsequent description of another, smaller-flowered form of *B. caudata* under the name of *B. longissima* var. *minor* (in Fedde Rep. Sp. Nov. Beih. 17:80. 1922).

77. MILTONIA Lindl.

MILTONIA Lindl. in Bot. Reg. 23: sub *t. 1976*. 1837; Benth. & Hook. Gen. Pl. 3:563. 1883.

? Gynizodon Raf. Fl. Tellur. 4:40. 1836.
Macrochilus Knowles & Westcott, Fl. Cab. 1:93, *t. 45*. 1837.

Epiphytic herbs, with short, usually rather inconspicuous, compressed pseudobulbs bearing 1–2 leaves at the apex, the base enveloped in few to many distichous, imbricating, conspicuously foliaceous bracts. Leaves and bract blades elliptic-lanceolate to narrowly linear, coriaceous to subcoriaceous, contracted at the base into short or elongate conduplicate petioles. Inflorescences axillary from the base of the pseudobulb, often short, erect or arching, 1- to few-flowered scapes or sometimes elongate, many-flowered racemes. Flowers relatively large and conspicuous, on long slender pedicels subtended by elongate, spathaceous, or sometimes minute and inconspicuous bracts, the perianth segments and the lip usually being all on one plane so that the flowers are typically flat. Sepals subequal, spreading, free, or the laterals very shortly connate at the base. Petals subequal to the sepals or a little broader. Lip entire, broadly spreading, the apex often bifid, the base sessile or very shortly and broadly clawed and affixed to the base of the column usually at a right angle, the disk inconspicuously or sometimes prominently lamellate. Column short, the apex or anterior portion variously 2-auriculate or 2-alate, the clinandrium short, truncate, or the apex 2-lobed, or sometimes membranaceous and dilated, 2- to 3-lobed, the base without a foot. Anther terminal, operculate, incumbent, 1- or imperfectly 2-celled; pollinia 2, waxy.

About 20 species of attractive, mostly highland epiphytes closely allied to *Oncidium* and *Odontoglossum*, having centers of development in the mountains of Colombia and southern Brazil, with a single species known from as far north as Costa Rica.

1. MILTONIA ENDRESII Nichols. in Dict. Gard. 2:368. 1888.

Odontoglossum Warscewiczii Rchb. f. in Bot. Zeit. 10:692. 1852.
Miltonia superba Schltr. in Fedde Rep. Sp. Nov. 3:249. 1907.

Erect, caespitose, epiphytic herbs with distichous, foliaceous stems 16–38 cm. tall, the conduplicate, imbricating leaf bases enveloping a small complanate, elliptic-oblong, monophyllous pseudobulb 3–5 cm. tall and 1.2–1.5 cm. wide. Leaves narrowly linear to lanceolate, obliquely acute to acuminate, coriaceous, the blades 12–30 cm. long and 1–2.5 cm. wide, contracted below into short or elongate conduplicate petioles. Inflorescences 1 or 2 erect or arching, 2- to 5-flowered racemes 15–30 cm. long, produced from the lateral bases of the pseudobulbs. Flowers large and conspicuous, on elongate pedicels, white with a rose-purple blotch at the base of the perianth segments and two blotches at the base of the lip, or sometimes entirely white with a golden yellow disk. Sepals broadly ovate, the laterals acute, the dorsal sepal usually obtuse with a minute apicule, 2.5–3 cm. long and 1–1.5 cm. wide. Petals a little broader than the sepals, spreading, elliptic-obovate, obtuse or minutely apiculate, about 2.5 cm. long and 1.2–1.6 cm. wide. Lip entire, broadly panduriform, 3–3.5 cm. long and 2.5–4 cm. wide, the apex broadly emarginate and 2-lobed, sometimes with a minute central mucro, the base of the lip with a very short, broad claw which is affixed at right angles to the base of the column, the disk with 3 short, fleshy, obtuse, puberulent keels. Column stout, 4–5 mm. long, the apex dilated, nearly wingless.

Costa Rica and Panama.

CHIRIQUÍ: trail from Paso Ancho to Monte Lirio, upper valley of the Río Chiriquí Viejo, 1500–2000 m., *Allen 1508*.

An attractive highland species, often forming clumps in the tops of the tallest forest trees. Our specimens have pure white flowers, with a yellow disk, and narrower leaves than in the Costa Rican material, but otherwise seem to be identical. Mr. Walter Cope, of Pedro Miguel, reports that *Miltonia Roezlii* Nichols., a lowland species of the Colombian Choco, has been found in the upper Madden Lake region.

78. ONCIDIUM Swartz

ONCIDIUM Sw. in Vet. Akad. Nya Handl. Stockh. 21:239. 1800; Lindl. Folia Orch. Oncidium, (1). 1855; Benth. & Hook. Gen. Pl. 3:562. 1883.

? Phadrosanthus Neck. Elem. 3:153. 1790.
Cyrtochilum HBK. Nov. Gen. & Sp. 1:349. 1815.
Cyrtochilos Spreng. Syst. Veg. 3:729. 1826.
Coppensia Dum. in Mem. Acad. Brux. 9:10. 1835, in nota.
Tolumnia Raf. Fl. Tellur. 2:101. 1836.
Xeilyathum Raf. loc. cit. 62. 1836.
Xaritonia Raf. loc. cit. 4:9. 1836.
Psychopsis Raf. loc. cit. 40. 1836.
Lophiaris Raf. loc. cit. 40. 1836.
Olgasis Raf. loc. cit. 51. 1836.
Palumbina Rchb. f. in Walp. Ann. 6:699. 1861.
Papiliopsis E. Morr. in Belg. Hortic. 24:261. 1874.
Baptistonia Barb. Rodr. Gen. & Sp. Orch. Nov. 1:95. 1877.

Erect or pendulous, epiphytic or infrequently terrestrial herbs with short, foliaceous stems, most frequently thickened into conspicuous, more or less ancipitous, 1- to 2 (rarely more)-leaved pseudobulbs, the bases enveloped in several papery or foliaceous bracts, or less frequently with the pseudobulbs very short, rudimentary, cylindric, subconic, or complanate-cylindric, enveloped in several papery sheaths, or the plants rarely with many distichously equitant leaves and entirely without pseudobulbs. Leaves subcoriaceous, coriaceous or fleshy, equitant, flat, terete or triangular. Inflorescences usually 1 or 2 short or elongate, often flexuose, erect, arching or laxly pendulous, branching panicles, simple racemes, or 1-flowered scapes produced from the lateral bases of the pseudobulbs, or in the equitant-leaved species from the axils of the leaves. Flowers often large and conspicuous, usually yellow or brown. Sepals usually subequal, spreading or reflexed, free, or the laterals somewhat connate rarely nearly to the apex, the dorsal sepal rarely much longer and narrower than the laterals. Petals subequal to the dorsal sepal or sometimes larger. Lip usually 3-lobed, often pandurate, rarely nearly entire, the base shortly clawed or sessile and adnate to the base of the column, usually forming a right-angle with it, the lateral lobes porrect, spreading or reflexed, sometimes obsolete, the central portion of the lip usually with an isthmus, the mid-lobe spreading, usually very broad and transversely dilated, rarely narrow, often emarginate or bifid, the disk usually conspicuously cristate or tuberculate. Column usually short, stout, the lateral margins near the stigma with or without auriculate or petaloid projections, the clinandrium very short and truncate or ovate and obliquely erect, entire or with the apex shortly bidentate, the base footless or sometimes apparently with a short foot, rarely produced into a prominent, erect, horn-like process. Anther terminal, operculate, incumbent, strongly convex, semiglobose or cucullate, 1-celled, imperfectly or rarely 2-celled; pollinia 2, usually deeply sulcate, waxy.

A very large, polymorphic genus of often attractive, usually epiphytic American orchids ranging from Florida and Mexico to the West Indies and South America as far as Peru, Bolivia, and Brazil. Twenty-six species are thus far known from Panama.

a. Plants without pseudobulbs, or the pseudobulbs rudimentary and inconspicuous.
  b. Leaves solitary, fleshy, from the apex of a very short subconic or subcylindric stem. Basal sheathing bracts papery.
    c. Leaves broadly lanceolate to elliptic-oblong..... 6. O. CARTHAGINENSE
  cc. Leaves terete.
    d. Lip more than twice as long as the lateral sepals. Basal callus occupying less than half of the total length of the isthmus.
      e. Flowers very small, the lip 1 cm. long or less, at the base with 2 separate and distinct keels ending in small tubercles on either side of the central boss..... 9. O. EBRACHIATUM
    ee. Flowers of moderate size, the lip 1 cm. long or more, at the base without keels or tubercles on either side of the prominent central boss..... 24. O. STIPITATUM
    dd. Lip less than twice as long as the lateral sepals. Basal callus very prominent, occupying nearly all of the central isthmus..... 25. O. TERES
bb. Leaves many, coriaceous or subcoriaceous, the conduplicate bases

distichously imbricating.
c. Plants dwarf, less than 10 cm. tall.
d. Leaves not equitant, the conduplicate bases enveloping a small pseudobulb. Peduncles filiform, not conspicuously flattened at the apex..... 8. O. CRISTA-GALLI
dd. Leaves equitant, the plants entirely without pseudobulbs. Peduncles conspicuously flattened, particularly near the apex..... 22. O. PUSILLUM
cc. Plants robust, more than 35 cm. tall.
d. Base of the lip with prominent, well-developed lateral lobes..... 17. O. OCHMATOCHILUM
dd. Base of the lip without prominent, well-developed lateral lobes.. 19. O. PANDURIFORME
aa. Plants with conspicuous pseudobulbs.
b. Lip conspicuously exceeding the lateral sepals in length.
c. Pseudobulbs suborbicular, about as broad as long.
d. Pseudobulbs very distantly inserted on an elongate, slender, flexuose rhizome..... 11. O. GLOBULIFERUM
dd. Pseudobulbs approximate on a short rhizome.
e. Bracts enveloping the base of the pseudobulb foliaceous.
f. Apex of the pseudobulb diphyllous..... 15. O. NEBULOSUM
ff. Apex of the pseudobulb monophyllous.
g. Apical leaf of the pseudobulb much reduced, conspicuously less than the bract blades in length..... 8. O. CRISTA-GALLI
gg. Apical leaf of the pseudobulb about equal to the bract blades in length.
h. Lip with a distinct rectangular isthmus..... 16. O. OBRYZATUM
hh. Lip with a sharp median constriction, but without a distinct rectangular isthmus..... 7. O. CHEIROPHORUM
ee. Bracts enveloping the base of the pseudobulb not foliaceous.... 1. O. AMPLIATUM
cc. Pseudobulbs elliptic-oblong to oblong-ovoid, usually more than twice as long as broad.
d. Pseudobulbs monophyllous at the apex. Sepals about 5 mm. long..... 20. O. PARVIFLORUM
dd. Pseudobulbs 2- to 3-leaved at the apex.
e. Inflorescences with both normal and abortive sterile flowers.... 12. O. HETERANTHUM
ee. Inflorescences with only normal fertile flowers.
f. Sepals obovate-spatulate, broadly obtuse or truncate..... 16. O. OBRYZATUM
ff. Sepals lanceolate to elliptic-lanceolate, acute to subacute.
g. Isthmus broad, at least half the width of the mid-lobe.... 5. O. CABAGRAE
gg. Isthmus narrow, usually less than ¼ the width of the mid-lobe..... 13. O. ISTHMI
bb. Lip subequal to the lateral sepals or shorter.
c. Lateral sepals connate nearly to the apex..... 26. O. WARSCEWICZII
cc. Lateral sepals free, or only very shortly connate at the base.
d. Dorsal sepal and petals elongate, linear-spatulate, very dissimilar to the broad lateral sepals. Flowers solitary, at the apex of an elongate scape..... 14. O. KRAMERIANUM
dd. Sepals and petals more or less similar in shape.
e. Floral bracts very large and conspicuous.
f. Flowers more than 3 cm. in diameter, the mid-lobe of the lip subequal to the dorsal sepal in width..... 21. O. POWELLII
ff. Flowers less than 3 cm. in diameter, the mid-lobe of the lip conspicuously exceeding the dorsal sepal in width..... 4. O. BRACTEATUM
ee. Floral bracts small or slender and inconspicuous.
f. Leaves narrowly linear-ligular, acute or acuminate. Pseudobulbs usually 2- to 3-leaved at the apex.
g. Lower portions of the foliaceous bracts not articulated, without a suture..... 10. O. ENSATUM
gg. Lower portions of the foliaceous bracts articulated, with a distinct suture.
h. Lip with a distinct isthmus, the callus with 2 crenulate or denticulate, lateral plates at the base..... 3. O. BAUERI
hh. Lip without a distinct isthmus, the callus surmounted by 4 divergent, crenulate keels..... 18. O. PANAMENSE
ff. Leaves broadly lanceolate, obtuse to subacute. Pseudobulbs usually monophyllous at the apex.

g. Lip distinctly shorter than the lateral sepals.
  h. Mid-lobe of the lip about equaling the dorsal sepal in width. Apex of the callus with a broad transverse plate..... 21. O. POWELLII
  hh. Mid-lobe of the lip conspicuously exceeding the dorsal sepal in width. Apex of the callus with 3 fleshy teeth.. 23. O. STENOTIS
gg. Lip about equaling the lateral sepals, or somewhat longer.
  h. Pseudobulbs exceptionally thin and flattened, without prominent longitudinal ridges, the conduplicate bases of the foliaceous bracts thin and papery..... 2. O. ANSIFERUM
  hh. Pseudobulbs not exceptionally thin and flattened, with prominent longitudinal ridges, the conduplicate bases of the foliaceous bracts coarsely fibrous..... 3. O. BAUERI

1. ONCIDIUM AMPLIATUM Lindl. Gen. & Sp. Orch. Pl. 202. 1833.

Oncidium Bernoullianum Kränzl. in Engler, Pflazenr. IV, Fam. 50 (Heft 80):231. 1922.

Epiphytic herbs with ovoid to suborbicular, strongly compressed, or sometimes angular, pseudobulbs which are often longitudinally ridged and transversely wrinkled, 3–12 cm. tall and 3–9 cm. wide, usually flecked with red or brown, rarely entirely raisin-purple, the apex with 1–3 leaves, the base enveloped in several papery, imbricating bracts. Leaves elliptic-oblanceolate to ligular, obtuse to subacute, coriaceous, 8–40 cm. long and 3–12 cm. wide, contracted below into short conduplicate petioles. Inflorescences 1 or 2 erect or arching, few- to many-flowered racemes or panicles conspicuously exceeding the leaves in length, produced laterally from the bases of the pseudobulbs. Flowers variable in size but averaging about 2.5 cm. in diameter, bright yellow, nearly white on the reverse surfaces, the sepals spotted with reddish brown, the callus white spotted red. Sepals free, subequal, spreading, oblong-spatulate, obtuse, the dilated apices deeply concave, 6–10 mm. long and 3.5–5 mm. wide. Petals much broader than the sepals, clawed at the base, with flat suborbicular blades, 7–11 mm. long and 5–9 mm. wide. Lip very broadly spreading, 3-lobed, 1.5–2 cm. long and 2–3 cm. wide, the lateral lobes relatively small, subauriculate, obtuse, the central portion of the lip with a short constriction, the mid-lobe abruptly dilated, deeply emarginate and 2-lobed, transversely oblong or reniform, the base of the lip contracted into a short claw and adnate to the base of the column, the disk with an erect, fleshy callus, surmounted by a transverse biauriculate plate and terminating at the apex in a prominent tridenticulate process. Column very short, 3–4 mm. long, the apex with 3 denticulate wings, the base without a foot.

Guatemala to Peru, Venezuela, and Trinidad.

CANAL ZONE: Chagres, sea level, *Fendler 331;* near Culebra, 50–100 m., *Pittier 3397;* Cruces, sea level, *Powell 3109;* Barro Colorado Island, Gatún Lake, *Woodworth & Vestal 706, Shattuck 203;* Frijoles, *Powell 3211;* McComber Hill, 300 ft., *Powell 3200.* PANAMÁ: near Bejuco, 100 ft., G. *Fairchild s. n.* COCLÉ: near La Pintada, 150 m., *Allen 3918.* VERAGUAS: Bahia Honda, *Taylor 1512.*

An attractive lowland species with bright yellow flowers, widely distributed in the American tropics. In Panama they were formerly very frequent in the Chagres River valley, and in general along streams where they were often found high on the trunks and branches of the common *Espavé (Anacardium excelsum).* The

Fig. 199. *Oncidium ampliatum*

larger-flowered forms are often offered for sale under the name of *Oncidium ampliatum* var. *majus*.

2. ONCIDIUM ANSIFERUM Rchb. f. in Bot. Zeit. 10:696. 1852.

Oncidium ensatum Hort. ex Rchb. f. in Xenia Orch. 1:232. 1858, in synon., non Lindl.
Oncidium hieroglyphicum Hort. pro parte ex Rchb. f. loc. cit. 1858, in synon.
Oncidium Lankesteri Ames, in Sched. Orch. 4:53. 1923.
Oncidium naranjense Schltr. in Fedde Rep. Sp. Nov. Beih. 19:259. 1923.

Epiphytic herbs with very strongly compressed, exceptionally thin, ovate-elliptic or oblong-elliptic, usually smooth pseudobulbs 6–10 cm. tall and 3–6 cm. wide, the apices with 1 or infrequently 2 leaves, the bases with several distichously imbricating bracts the uppermost 2–3 of which are conspicuously foliaceous. Leaves lanceolate to elliptic-lanceolate, subacute to obtuse, pergameneous, 15–33 cm. long and 2.5–5.5 cm. wide. Inflorescences 1 or 2 erect or arching panicles, usually much exceeding the leaves, up to about 1 m. in length, produced from the lateral bases of the pseudobulbs. Flowers of moderate size, averaging about 3 cm. in diameter, the sepals and petals brown, sometimes with yellow margins and apices, the mid-lobe and lateral lobes of the lip bright yellow, the central isthmus brown with a bright yellow crest. Sepals subequal, free, spreading, elliptic-lanceolate, obtuse to acute, with strongly undulate margins, 1.2–1.7 cm. long and 0.4–0.6 cm. wide. Petals somewhat broader than the sepals, spreading, elliptic-oblong, obtuse to subacute, with undulate margins, 1.4–1.6 cm. long and 0.5–0.65 cm. wide. Lip pandurate, 3-lobed, 1.4–1.6 cm. long and 1–1.5 cm. broad at the transversely reniform, emarginate apex, the mid-section of the lip abruptly contracted in front into a broad isthmus, the basal portions more or less confluent with the short, suborbicular, lateral lobes, the disk with a 5-lobed puberulous crest, terminating in a central porrect tooth. Column short, 4–6 mm. long, the apex with dolabriform wings.

Costa Rica and Panama.

CHIRIQUÍ: Río Chiriquí Viejo, vicinity Paso Ancho, 5000 ft., *H. Dunn s. n.*; Llano del Volcán, western slopes of Chiriquí Volcano and along Río Chiriquí Viejo, 1200 m., *Allen 1011*.

An attractive highland species, readily distinguished from other Panama Oncidiums by the broad, smooth, exceptionally thin pseudobulbs.

3. ONCIDIUM BAUERI Lindl. in Bauer & Lindl. Ill. Orch. Gen. *t. 7.* 1830-38.

Oncidium altissimum var. β Lindl. Gen. & Spec. Orch. Pl. 200. 1833.
Epidendrum gigas L. C. Rich. ex Lindl. loc. cit. 200. 1833.
Oncidium altissimum Lindl. in Bot. Reg. 19: *t. 1651*. 1833, non Sw.
Oncidium polycladium Rchb. f. ex Lindl. Fol. Orch. Oncidium, (47). 1855.
Oncidium altissimum var. *Baueri* Stein, Orchideenb. 404. 1892.

Erect, robust, epiphytic herbs with approximate, oblong-ovoid, strongly ridged pseudobulbs up to about 18 cm. tall and 4 cm. wide, the apices with 1 or 2 leaves, the lower portions enveloped in the coarsely fibrous, conduplicate, imbricating

bases of several conspicuously foliaceous bracts. Leaves and bract blades linear-ligular, acute, subcoriaceous, up to about 75 cm. long and 2.5–4 cm. wide. Inflorescences 1 or 2 stout, erect, arching or pendulous, many-flowered panicles up to about 3 m. in length, produced from the lateral bases of the pseudobulbs. Flowers of moderate size, 2.5–3 cm. in diameter. Sepals free, subequal, spreading or reflexed, shortly clawed at the base, yellow marked with brown, the dorsal sepal elliptic-lanceolate, acute, 1–1.5 cm. long and 0.4–0.5 cm. wide, the lateral sepals obliquely linear-lanceolate, acute or shortly acuminate, the dorsal surface with a distinct central keel, 1.2–1.7 cm. long and 0.35–0.45 cm. wide. Petals subequal to the dorsal sepal and similarly colored, elliptic-lanceolate, acute, with undulate margins, 1–1.4 cm. long and about 0.5 cm. wide. Lip pandurate, 3-lobed, yellow with a reddish brown central blotch, 1.2–1.5 cm. long and 0.9–1.2 cm. wide, the lateral lobes small, suborbicular to subquadrate, obtuse, the central portion of the lip contracted into a distinct isthmus, the mid-lobe abruptly dilated, emarginate and bilobed, transversely reniform in outline, the disk with an erect, fleshy callus, at the base with 2 lateral crenulate or denticulate wings or plates, the apex with 3 short, fleshy teeth. Column about 5 mm. long, with the lateral wings often bifid, the lower lobules obtuse and spreading, the apices acute or acuminate, often more or less converging.

Mexico to Brazil and Peru; Virgin Islands and Martinique.

PANAMÁ: without definite locality, Pacific coast lowlands, *Fairchild s. n.* CHIRIQUÍ: without definite locality, *von Warscewicz s. n.* (fide Reichenbach).

The species of this type form a closely allied, very perplexing association including *Oncidium altissimum* Sw., *O. Baueri* Lindl., *O. sphacelatum* Lindl., *O. polycladium* Rchb. f., *O. stenotis* Rchb. f., *O. isthmi* Schltr., and *O. panamense* Schltr. *Oncidium stenotis* and *O. isthmi* can be separated easily, and although *O. sphacelatum* and *O. panamense* are very nearly alike, they differ from the other species in the broad basal half of the lip, without a distinct isthmus. The most troublesome series involves the remaining species, which have a broad but distinct isthmus to the lip, a transversely reniform mid-lobe, and variously developed multi-denticulate basal calli. These are extremely difficult to distinguish from one another, at least on the basis of herbarium material, since most of the described differences consist more nearly in the degree of development of essentially identical parts, rather than in any basic structural deviation. In particular, there seem to be no consistent characters upon which to base the further segregation of *O. polycladium* from *O. Baueri*, the former concept being here reduced to synonymy, thus extending the range of the widespread South American and West Indian *O. Baueri* as far north as Mexico. In our material, the latter species is separable from *O. panamense* by the distinct isthmus of the lip; from *O. isthmi* by the broader isthmus and narrower, shorter mid-lobe; and from *O. stenotis* by the smaller flowers, in which the lip is about equal to the lateral sepals in length. It seems quite probable that further study may reduce some of these, and other closely allied concepts, to varietal status or synonymy.

4. ONCIDIUM BRACTEATUM Warsc. & Rchb. f. in Bot. Zeit. 10:695. 1852.

Erect, epiphytic herbs with slender brown, compressed pseudobulbs, more or less linear in outline but usually somewhat broader at the base and tapering gradually to a narrower apex, 6–12 cm. tall and 1.5–3 cm. wide at the base, terminating above in 1 or 2 leaves, the base enveloped in several distichously imbricating bracts, the uppermost 2 or 3 of which are conspicuously foliaceous. Leaves ligular, obtuse, coriaceous, 15–45 cm. long and 2–3.2 cm. wide, contracted below into elongate, slender, conduplicate petioles. Inflorescences 1 or 2 erect or arching panicles much exceeding the leaves, up to about 1 m. in length, the lateral branches short, usually 3-flowered, provided with several conspicuous, elongate, acute, pale brown, spathaceous bracts. Flowers of moderate size, the sepals and petals greenish yellow or yellow, heavily blotched and spotted dark brown or maroon, the apical and lateral lobes of the lip bright yellow, the central isthmus brown or maroon. Sepals subequal, free, spreading, with undulate margins, the dorsal sepal oblong-lanceolate, acute, 10–15 mm. long and 3.5–5 mm. wide, the lateral sepals linear-lanceolate, obliquely acute, with a distinct central keel on the dorsal surface, 12–17 mm. long and 2.5–4.5 mm. wide. Petals subequal to the dorsal sepal, elliptic-lanceolate, acute, with undulate margins, 10–15 mm. long and 4–6 mm. wide. Lip panduriform, with a broad central isthmus, 12–15 mm. long and 10–12 mm. wide at the 2-lobed emarginate apex, the base with 2 small, suborbicular, lateral auricles, the disk with an erect, more or less triangular, multidenticulate callus. Column 5–6 mm. long, with narrow lateral wings, the base without a foot.

Costa Rica and Panama.

Although absent from recent collections in our area, the species was originally described from plants presumably found in Panama by von Warscewicz, the data being given as "Chiriquí Cordilleren 6–9000 ft. auf Bäumen." They are readily distinguished by the narrow brown pseudobulbs and the very conspicuous, pale brown, spathaceous floral bracts.

5. ONCIDIUM CABAGRAE Schltr. in Fedde Rep. Sp. Nov. 9:292. 1911.

Oncidium Rechingerianum Kränzl. in Engler, Pflanzenr. IV, Fam. 50 (Heft 80):202, *fig. 18, C:a-c.* 1922.

Erect, epiphytic herbs with slender, elliptic-ovoid to nearly linear, ancipitous pseudobulbs usually 6–11 cm. tall and 2–3 cm. wide, densely spotted dark brown or black, often becoming longitudinally ridged with age, the apex with 2 or 3 leaves, the lower portions enveloped in the conduplicate bases of several distichously imbricating bracts, the uppermost 2 or 3 of which are conspicuously foliaceous. Leaves ligular, acute, subcoriaceous, 15–25 cm. long and 1.5–3 cm. wide, contracted below into slender, conduplicate petioles. Inflorescences usually solitary, erect or arching, many-flowered panicles much exceeding the leaves, up to about 80 cm. in length, produced from the lateral bases of the pseudobulbs. Flowers of moderate size, the sepals and petals heavily blotched rich chestnut-brown, usually

with yellow margins and apices, the mid-lobe and lateral lobules of the lip bright yellow with the central isthmus a rich reddish brown, the callus white spotted with brown. Sepals subequal, free, usually reflexed, with recurved apices, the dorsal sepal elliptic-obovate, acute, usually 8–12 mm. long and 4–6 mm. wide, the laterals linear-lanceolate to rather obliquely ligular, subacute to acute, with a distinct dorsal keel, usually 8–12 mm. long and 3–4 mm. wide. Petals somewhat broader than the sepals, slightly reflexed, with rather undulate margins, elliptic-oblanceolate, obtuse or acute, usually 10–12 mm. long and 5–6 mm. wide. Lip pandurate, usually 12–16 mm. long and 10–14 mm. wide at the 2-lobed, emarginate apex, the central portion abruptly contracted into a broad isthmus, the base with 2 small, lateral, obtuse, subquadrate auricles, the disk with an erect, fleshy, truncate keel, the upper margins with 2 pairs of fleshy teeth, the basal pair larger than the apical pair. Column short, erect, about 5 mm. long, with broad, lateral, spreading, rather bilobed or minutely dentate wings, the base of the column without a foot.

Costa Rica and Panama.

COCLÉ: region north of El Valle de Antón, 1000 m., *Allen 2361, 3681, 3776;* mountains beyond La Pintada, 400–600 m., *Hunter & Allen 589.* CHIRIQUÍ: without definite locality, 4000–5000 ft., *Powell 161, 177;* vicinity Palo Alto, 4000 ft., *Powell 301;* Llano del Volcán, 1000 m., *Kieswetter s. n.*

An attractive species of the Coclé and Chiriquí highlands, usually found growing in the tops of tall trees.

6. ONCIDIUM CARTHAGINENSE (Jacq.) Sw. in K. Vet. Akad. Stockh. Nya Handl. 21:240. 1800.

Epidendrum carthaginense Jacq. Select. Stirp. Amer. 228, *t. 133, fig. 4.* 1763.
Epidendrum undulatum Sims, in Bot. Mag. *t. 777.* 1804.
Oncidium undulatum Salisb. in Trans. Roy. Hort. Soc. 1:295. 1812, non Lindl.
Oncidium panduriferum Kunth, in HBK. Nov. Gen. & Spec. 1:346, *t. 82.* 1815.
Oncidium Oerstedii Rchb. f. in Bonplandia 2:91. 1854.
Oncidium carthaginense (Jacq.) Sw. var. *Oerstedii* (Rchb. f.) Lindl. Fol. Orch. Oncid. (40). 1855.
Oncidium carthaginense (Jacq.) Sw. var. *Swartzii* Lindl. loc. cit. 1855.
Oncidium obsoletum Rich. et Gal. ex Lindl. loc. cit. 41. 1855.
Oncidium kymatoides Kränzl. in Engler, Pflanzenr. IV, Fam. 50 (Heft 80):112. 1922.
Oncidium Oerstedii Rchb. f. var. *crispiflorum* Schltr. in Fedde, Rep. Sp. Nov. Beih. 17:85. 1922.

Robust, epiphytic herbs with very short, subquadrate, compressed or subcylindric, nearly obsolete pseudobulbs 1–2 cm. long and 1–1.5 cm. broad, the truncate apex with a single persistent, broadly lanceolate to elliptic-oblong, acute, usually fleshy leaf, which usually is more or less spotted reddish brown, 15–60 cm. long and 3.5–8 cm. wide, the lower surface with a strongly developed central keel, the pseudobulbs and the bases of the new leaves enveloped in 3–4 papery, closely imbricating bracts. Inflorescences elongate, erect, usually solitary, arching or sometimes pendulous, many flowered panicles up to 1.5 m. in length, produced from the bases of the pseudobulbs. Flowers variable in size and color, averaging

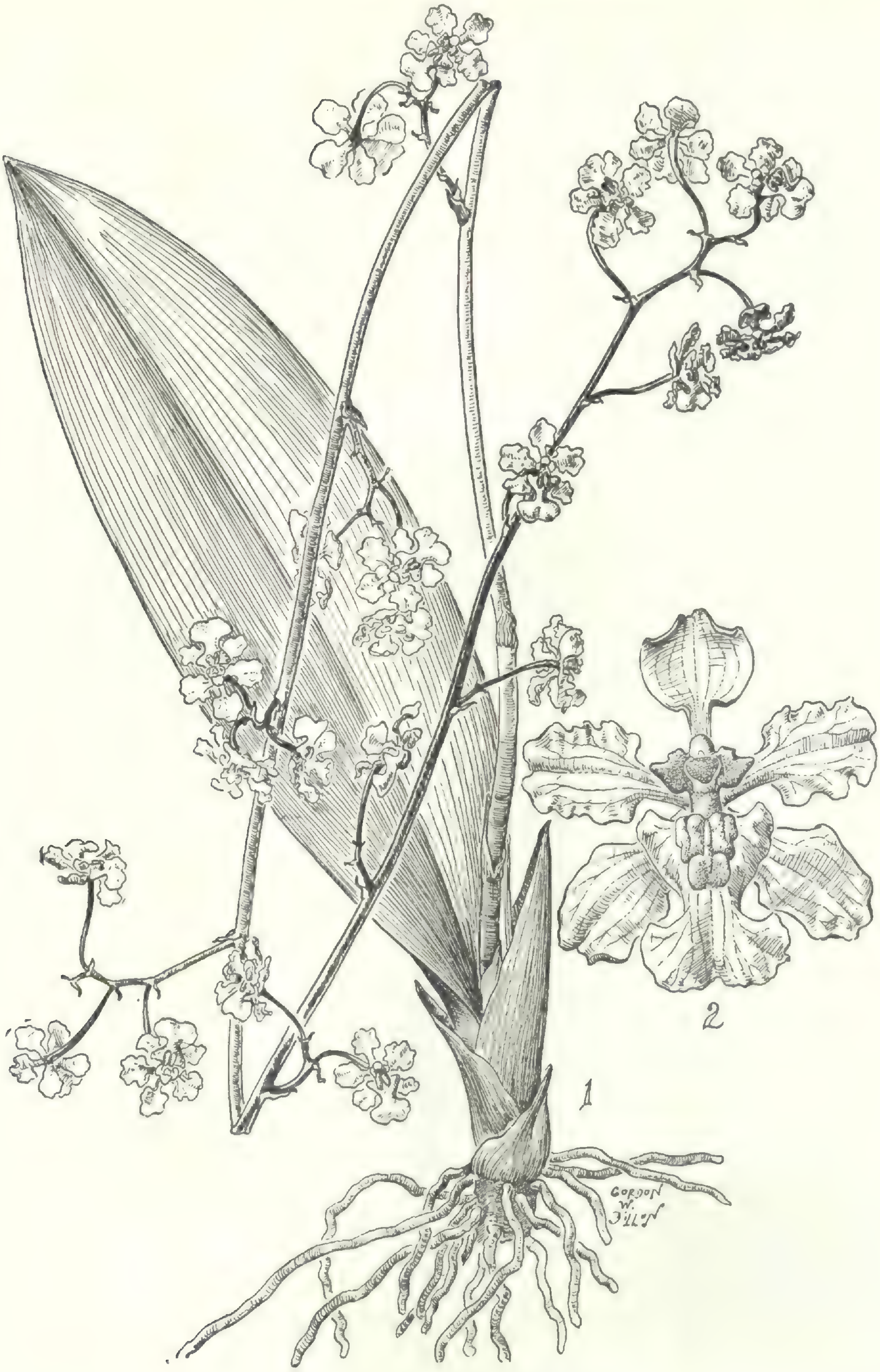


Fig. 200. *Oncidium carthaginense*

about 2 cm. in diameter, usually more or less heavily blotched and spotted with purplish rose on a white base. Sepals of about equal length, spreading, or with the laterals somewhat reflexed, distinctly clawed at the base, the blades with strongly undulate margins, the dorsal sepal free, the claw narrowly linear, the blade abruptly dilated and suborbicular, somewhat concave, 8–11 mm. long and 5–7 mm. wide, the lateral sepals very shortly connate at the base, the blades obovate-spatulate, obtuse to acute, 7–12 mm. long and 4–6 mm. wide. Petals distinctly clawed at the base, spreading, with undulate, often crisped margins, the blades oblong to elliptic-oblong, obtuse, 8–12 mm. long and 5–7 mm. wide. Lip pandurate in outline, 3-lobed, abruptly contracted at the base and adnate to the base of the column, 8–12 mm. long and 6–10 mm. wide, the mid-lobe transversely subreniform, the anterior margin entire or sometimes shallowly emarginate, the central portion of the lip with a median constriction often prolonged into a short, broad isthmus confluent at the base with the oblong, obtuse, or triangular, rather auriculate lateral lobes, which are often somewhat reflexed, the disk with a prominent, more or less 4-parted, fleshy, erect, tuberculate crest. Column 2–3 mm. long, with large, spreading, unequally 2-lobed, lateral wings.

Florida and the West Indies; Mexico to Venezuela and Brazil.

CANAL ZONE: vicinity Fort Kobbe, on margins of mangrove swamps, sea level, *Allen 2754*. PANAMÁ: margin of the Pacific Ocean, northwest of Panama City, on slope of hill rising from the sea, *Powell 1*. CHIRIQUÍ: near city of David, sea level, *Powell 270*.

A rather variable species closely allied to *Oncidium guttatum* (L.) Rchb. f., widely distributed in the lowlands of the American tropics. Most of the available specimens from Panama would correspond fairly well to the concept of *O. carthaginense* var. *Oerstedii*, yet the supposed differences (shorter lip, longer isthmus, and brighter coloring) are found in an extensive series of specimens from the entire geographic range to merge imperceptibly with the type, leaving no clear-cut grounds for separation.

7. ONCIDIUM CHEIROPHORUM Rchb. f. in Bot. Zeit. 10:695. 1852.

Oncidium Dielsianum Kränzl. in Engler, Pflanzenr. IV, Fam. 50 (Heft 80):197, *t. 17, fig. F; a-b.* 1922.

Dwarf, caespitose, epiphytic herbs averaging 12–15 cm. in height, with ovoid to suborbicular, compressed, monophyllous or rarely diphyllous pseudobulbs 1.5–3 cm. long and 1.4–2.5 cm. wide, at first smooth, often becoming finely wrinkled with age, the bases enveloped in several imbricating bracts the uppermost 2 or 3 of which are conspicuously foliaceous. Leaves linear-ligular, obtuse to subacute, pergameneous, 5–15 cm. long and 0.8–1.4 cm. wide, contracted below into short, conduplicate petioles. Inflorescences 1 or 2 slender, erect or arching, densely paniculate scapes usually exceeding the leaves, up to about 30 cm. in length, produced from the lateral bases of the pseudobulbs. Flowers small, averaging 1–1.5 cm. in diameter, bright yellow and fragrant. Sepals of about equal length, the dorsal sepal erect, shortly clawed at the base, the orbicular blade deeply concave,

often with a minute apicule, about 5 mm. long and 4 mm. wide, the lateral sepals elliptic-obovate, obtuse, often reflexed, apparently very shortly connate at the base, 5–6 mm. long and 3–3.5 mm. wide. Petals shortly clawed, spreading, obovate-spatulate, obtuse, about 4–5 mm. long and 4 mm. wide. Lip conspicuously 3-lobed, averaging about 8 mm. long and 12 mm. wide, the sessile base adnate to the base of the column, the broadly spreading, auriculate, lateral lobes subquadrate to suborbicular, usually with reflexed margins, the central portion of the lip with an abrupt, narrow constriction, the mid-lobe transversely subreniform or 2-lobed, the lobules often porrect in natural position, the disk with a prominent, fleshy keel, the upper margins with 2 conspicuous subquadrate wings, between which at the apex there is a short membranaceous hood or concavity. Column very short, with large obovate, usually porrect, lateral wings, the base produced in front into a prominent, erect, fleshy horn. Anther with a long beak, otherwise typical of the genus.

Costa Rica, Panama, and Colombia.

COCLÉ: El Valle de Antón, 500–1000 m., *D. Allen 3987, Hunter & Allen 350, Allen 236, 1681, 2914, 2939, 4211.* CHIRIQUÍ: without definite locality, 5000 ft., *Powell 54;* Volcancitos, 5500 ft., *Davidson 1261;* Piedra de Lino, 1600 m., *Killip 3571;* valley of the upper Río Chiriquí Viejo, near Monte Lirio, 1300–1900 m., *Seibert 224;* trail from Paso Ancho to Monte Lirio, Río Chiriquí Viejo, 1500–2000 m., *Allen 1499.*

A small-flowered, dwarf, but attractive species very common in the highlands of Coclé and Chiriquí provinces in our area, where the plants often form dense clumps in the tops of tall trees or on the ends of spreading branches, often fully exposed to the sun.

8. ONCIDIUM CRISTA-GALLI Rchb. f. in Bot. Zeit. 10:697. 1852.

Oncidium iridifolium Lindl. in Bot. Reg. 22: *t. 1911.* 1836, non HBK.
Oncidium decipiens Lindl. Folia Orch. Oncidium, (22). 1855.

Dwarf, caespitose, epiphytic herbs less than 10 cm. tall, with small, ovoid, compressed pseudobulbs 10–20 mm. tall and 8–18 mm. wide, the apices with a single very short, conduplicate, ensiform, abortive leaf sometimes reduced to a very abbreviated foliaceous apicule, 2–15 mm. long and 1–2 mm. wide, the bases of the pseudobulbs almost completely enveloped by the distichously imbricating, conduplicate bases of 4 to 6 conspicuous, foliaceous bracts, the blades ligular, acute, pergameneous, 2–8 cm. long and 0.5–1.0 cm. wide, usually explanate but sometimes conduplicate and ensiform. Inflorescences 1 to 4 erect or arching, filiform, 1-flowered scapes about equaling the leaves in length, produced from the axils of the foliaceous bracts, the peduncles provided with 3 or 4 distant, perfoliate, acuminate, spathaceous bracts 6–10 mm. long and about 3 mm. broad. Flowers very large in relation to the size of the plant, 2–3 cm. long and 1.8–2.2 cm. wide. Sepals free, spreading, the dorsal sepal erect, elliptic-ovate, slightly concave with a dorsal keel, terminating in a short apicule, the blade greenish yellow, 5–6 mm.

Fig. 201. *Oncidium crista-galli*

long and 3–4 mm. wide, the lateral sepals very inconspicuous, appressed to the back of the lip, rather obliquely linear-ligular, acuminate, greenish yellow, 5–6 mm. long and 2–2.5 mm. wide. Petals broadly spreading, oblong, rather obliquely obtuse and apiculate, bright yellow with transverse bands of reddish brown, the margins often undulate, 8–10 mm. long and 4–5 mm. wide. Lip complexly 3-lobed, 1.5–2.2 cm. long and 1.7–2.2 cm. wide, bright yellow, the margins undulate, the base shortly contracted and adnate to the base of the column, the lateral lobes spreading, obovate-spatulate, the dilated suborbicular blades 7–8 mm. long and 6–8 mm. wide, the mid-lobe much broader at the base than at the apex, divided into 4 lobules, the lateral basal pair rounded and spreading, the apical pair projecting, obliquely cuneate, separated by a deep central sinus, the disk convex, white with reddish brown blotches, with a prominent, spreading, fleshy, suborbicular plate and ruffled and crisped margins, subtended on each side by semicircular, crisped extensions, the apex terminating in a short, complex, crisped, fleshy hood. Column very short, about 3 mm. long, with conspicuous, lateral, dolabriform wings.

Mexico to Colombia and Peru.

COCLÉ: mountains beyond La Pintada, 400–600 m., *Hunter & Allen 588;* El Valle de Antón, 600–1000 m., *D. Allen 5158, Allen & Allen 1251, 1675, 2883, 3809.*

A remarkable, attractive, dwarf species of the wet highland forests of Coclé Province, with relatively large, bright yellow flowers, the plants superficially reminiscent of those of *Oncidium pusillum,* but readily distinguished by the presence of small suborbicular pseudobulbs and the filiform, rather than complanate, scapes.

9. ONCIDIUM EBRACHIATUM A. & S. in Sched. Orch. 8:75, *fig. 6.* 1925.

Pendulous, epiphytic herbs with fleshy, terete, longitudinally sulcate, acuminate leaves up to about 60 cm. in length, the plants identical in appearance with those of *Oncidium stipitatum*. Inflorescences usually solitary, arching, many-flowered panicles, produced from the bases of the plants. Flowers very small for the genus, about 1 cm. in length, the sepals and petals spotted with reddish brown, the lip yellow on both surfaces. Sepals free, spreading, the dorsal sepal suborbicular, strongly concave, incurving over the column, with an obscure, terminal apicule, the blades 3–3.5 mm. long and about 2.5 mm. wide, the lateral sepals obovate-spatulate, obtuse, minutely apiculate, the blades somewhat concave and incurving, about 4 mm. long and 2–2.2 mm. wide. Petals widely spreading, rather obliquely elliptic-oblong, obtuse, about 4 mm. long and 2–2.1 mm. wide. Lip pandurate, 3-lobed, about 8 mm. long and 6 mm. wide, the sessile base adnate to the base of the column, the lateral lobes subfalcate, obtuse, spreading, or with the apices somewhat antrorse in natural position, the lower margins confluent with the narrow central isthmus, the mid-lobe dilated and emarginate, flabellate-reniform in outline, often porrect in natural position, the minutely papillose disk with a broad, fleshy, flat, lunate, porrect plate below the column, terminating below the apex in a central, subtrilobed tubercle, on each side of which are lightly converging keels, terminating in low tuberculate swellings. Column very short and stout, about 1 mm. long, without prominent lateral wings.

Panama.

PANAMÁ: without definite locality, *M. D. Hunter s. n.;* coastal swamps east of Panama City, between the Jagua Hunt Club and Congor Hill, sea level, *Hunter & Allen 471;* San José Island, Perlas Archipelago, *Johnston 1340.* DARIÉN: Cana and vicinity, 2000–6500 ft., *R. S. Williams 975;* Río Tuira, near Pinogana, 100 ft., *Allen 4309.*

A small-flowered, terete-leaved species very closely allied to *O. nudum* Lindl. of South America; apparently confined to the lowlands of the eastern half of Panama.

10. ONCIDIUM ENSATUM Lindl. in Bot. Reg. n. s. 5: Misc. 17. 1842.

Oncidium cerebriferum Rchb. f. in Bot. Zeit. 10:696. 1852.
Oncidium confusum Rchb. f. in Xenia Orch. 1:234. 1858.

Erect, terrestrial herbs with fleshy, ovoid, somewhat compressed, usually smooth pseudobulbs 5.5–8 cm. tall and 3.5–5 cm. wide, the truncate apices with 1 to 3 leaves, the bases enveloped in 4–6 imbricating bracts the uppermost 2 or 3 of which are conspicuously foliaceous, the blades persistent, not articulated and not separating by a suture near the base. Leaves and bract blades linear-lanceolate, acuminate, subcoriaceous, 45–90 cm. long and 2–3 cm. wide, rather rigidly erect, with a strong central keel, the margins somewhat conduplicate, particularly for the lower half. Inflorescences 1 or 2 erect or arching, many-flowered panicles equaling or exceeding the leaves, produced from the lateral bases of the pseudo-

bulbs. Flowers of moderate size, in fresh material averaging about 3 cm. in diameter when spread out. Sepals subequal, free, spreading or reflexed, greenish or brownish olive, usually with undulant margins, the dorsal sepal oblanceolate, acute, 10–12 mm. long and 4–5 mm. wide, the lateral sepals lanceolate, acuminate, 13–15 mm. long and 3.5–4 mm. wide, with a pronounced dorsal keel. Petals subequal to the dorsal sepal and similarly colored, spreading or reflexed, with undulant margins, obliquely oblanceolate, acute, 12–14 mm. long and 4–5 mm. wide. Lip panduriform, 3-lobed, bright yellow, about 1.5 cm. long and 1.5 cm. wide, abruptly contracted at the base and adnate to the base of the column, the small lateral lobes oblong, obtuse or obscurely auriculate, the anterior margins confluent with the margins of the broad central isthmus, the mid-lobe dilated, 2-lobed, transversely subreniform, the disk olive-green, with a prominent, fleshy, white, 7-toothed callus. Column short, with prominent, lateral wings.

British Honduras to Panama.

PANAMÁ: foothills east of Panama City, sea level, *Powell 267;* vicinity Juan Díaz, *Powell 3484;* in low thick scrub, along Río Tecúmen, east of Panama City, about 30 m., *Hunter & Allen 266, Allen 5159.*

A fairly common terrestrial species of the Pacific slope, often found growing in low scrub in association with *Peristeria elata*, or sometimes in open grassland. In herbarium specimens, the species considerably resembles *Oncidium panamense*, but may be distinguished readily by the narrower basal callus, the terrestrial habit, and in the complete lack of articulations near the bases of the foliaceous bracts.

11. ONCIDIUM GLOBULIFERUM HBK. Nov. Gen. & Sp. 1:347. 1815.

Oncidium scansor Rchb. f. in Linnaea 22:844. 1849.
Oncidium convolvulaceum Lindl. in Paxt. Flow. Gard. 1:102, sub *t. 21.* 1850-51.
Oncidium globuliferum HBK. var. *costaricense* Rchb. f. in Gard. Chron. 1678. 1871.
Oncidium Wercklei Schltr. in Fedde Rep. Sp. Nov. Beih. 19:68: 1923.

Epiphytic herbs with solitary or clustered, elliptic-oblong to suborbicular, compressed, monophyllous pseudobulbs 1.2–2.5 cm. long and 1–2 cm. wide, very distantly distributed along the slender, flexuose, scandent rhizomes, the bases of the pseudobulbs partially enveloped in the conduplicate bases of several distichously imbricating bracts the uppermost pair of which being conspicuously foliaceous. Leaves elliptic-oblong to elliptic-lanceolate, obtuse to subacute, coriaceous, 2.5–6 cm. long and 1–2 cm. wide, contracted below into very short, conduplicate petioles. Inflorescences 1 or 2 short, erect, 1-flowered scapes about equaling the leaves in length, produced from the lateral bases of the pseudobulbs. Flowers very large in relation to the size of the plant, 2.5–3 cm. long and 2–2.5 cm. wide. Sepals free, spreading, yellow barred with reddish brown, the dorsal sepal elliptic-oblong, shortly acute, 8–12 mm. long and 4–5 mm. wide, the lateral sepals rather obliquely lanceolate, acute, 10–12 mm. long and 3–4 mm. wide. Petals somewhat broader than the sepals, yellow with reddish brown bars, elliptic-oblong, obtuse to subacute, 10–12 mm. long and 5–6 mm. wide. Lip 3-lobed, broadly spreading,

Fig. 202. *Oncidium globuliferum*

1.7–2 cm. long and 2–2.5 cm. wide, abruptly contracted at the base and adnate to the base of the column, the small subquadrate, auriculate, obtuse, lateral lobes spreading, the anterior margins confluent with the margins of the short, broad, central isthmus, the mid-lobe spreading, emarginate, 2-lobed, broadly and transversely reniform, bright yellow, about ⅔ the total length of the lip, the disk with a more or less triangular, 7-toothed, fleshy callus. Column short, about 5 mm. long, with a pair of spreading lateral wings.

Costa Rica to Venezuela and Peru.

COCLÉ: region north of El Valle de Antón, 1000 m., *Allen 5201*. CHIRIQUÍ: vicinity Bajo Mono and Quebrada Chiquero, 1500 m., *Woodson & Schery 572;* without definite locality, 5000 ft., *Kieswetter s. n.;* vicinity Cerro Punta, headwaters of the Río Chiriquí Viejo, 2000 m., *Allen 1567*.

Unique among the Oncidiums of Panama in having elongate, slender, flexuose rhizomes, the plants often forming large tangled colonies in the tops of tall trees in the wet highland forests. They are seldom seen except as fragments which have fallen from above, usually being rendered conspicuous by the yellowish rhizomes which superficially resemble the stems of a dodder. The solitary flowers are bright yellow, very large in relation to the size of the plant, often exceeding the pseudobulbs in diameter.

12. ONCIDIUM HETERANTHUM Poepp. & Endl. Nov. Gen. & Sp. 1:34, *t. 60*. 1836.

Oncidium bryolophotum Rchb. f. in Gard. Chron. 738. 1871.
Oncidium ionops Cogn. & Rolfe in Jour. des Orchid. 3:346. 1892.
Oncidium megalous Schltr. in Fedde Rep. Sp. Nov. 9:30. 1910.

Erect, caespitose, epiphytic herbs with linear or narrowly ovoid, rather compressed pseudobulbs up to about 5 cm. tall and 2 cm. wide, the truncate apices with 1 or 2 leaves, the bases enveloped in several imbricating bracts the uppermost 2 of which are conspicuously foliaceous. Leaves narrowly linear to elliptic-lanceolate, acute, subcoriaceous, 4–18 cm. long and 0.8–3.5 cm. wide, contracted below into very short conduplicate petioles. Inflorescences 1 or 2 slender, erect or arching panicles usually much exceeding the leaves, up to about 75 cm. long. Flowers dimorphic, each lateral branch of the inflorescences terminating in a single normal flower averaging about 2 cm. long and 1.2 cm. wide, subtended by many very dissimilar, small, stelliform, abortive, sterile flowers. Perianth segments of the sterile flowers broadly spreading, narrowly linear to spatulate, yellowish, 3–4 mm. long, the lip generally entirely aborted. Normal flowers with the sepals free, elliptic-lanceolate to ligular, shortly acute to obtuse, the bases shortly clawed, the blades often with undulate margins, yellow blotched with reddish brown, 6–10 mm. long and 2–3 mm. wide. Petals elliptic-oblong to obliquely obovate-spatulate, obtuse to subacute, clawed at the base, yellow blotched with reddish brown, 7–10 mm. long and 2.5–3.5 mm. wide. Lip broadly panduriform, 10–12 mm. long and 10–15 mm. wide, subequally 4-lobed, the lateral lobes broadly triangular,

obtuse, or rounded, the anterior margins converging and forming a short isthmus or narrow, median constriction above the abruptly dilated, spreading, transversely reniform, 2-parted, bright yellow mid-lobe, the disk with an erect, fleshy, tuberculate callus terminating at the apex in 3 short teeth. Column short, 3–4 mm. long, with 2 very prominent lateral wings.

Costa Rica, Panama, Colombia, Peru, Bolivia, and probably adjacent territories.

CHIRIQUÍ: without definite locality, "On large trees, in dense shade", 5000 ft., *Kieswetter s. n.*, *Powell 48;* central valley of the Río Chiriquí Viejo, vicinity of New Switzerland, 1800–2000 m., *Allen 1381.*

A curious highland species distinguished by the abundant yellowish, stelliform, abortive florets, subtending the normal flowers on the branches of the paniculate inflorescences.

13. ONCIDIUM ISTHMI Schltr. in Fedde Rep. Sp. Nov. Beih. 17:84. 1922.

Robust, erect, epiphytic herbs with approximate, narrowly ovoid to linear-oblong, compressed, longitudinally ridged, usually diphyllous pseudobulbs 8.5–12 cm. long and 3–4 cm. wide, the lower portions enveloped in the conduplicate, distichously imbricating bases of 6–7 bracts, the uppermost 4–5 of which are conspicuously foliaceous. Leaves and bract blades linear-lanceolate, acute, subcoriaceous, 15–45 cm. long and 1.5–3.2 cm. wide, the foliaceous bracts articulated near the base, with a distinct suture, the blades ultimately deciduous. Inflorescences 1 or 2 erect or arching, many-flowered panicles up to about 1 m. in length, produced from the lateral bases of the pseudobulbs. Flowers of moderate size, 2.5–3 cm. long and 1.5–2.2 cm. wide. Sepals free, spreading, clawed at the base, yellow barred with brown, the dorsal sepal elliptic-oblong, acute, with undulate margins, 9–12 mm. long and 4–5 mm. wide, the lateral sepals obliquely oblong, subacute, with undulate margins, 10–13 mm. long and 4–5 mm. wide. Petals rather obliquely oblong, subacute, with undulate margins, yellow barred with brown, 10–12 mm. long and 4–5 mm. wide. Lip panduriform, 3-lobed, bright yellow, the small auriculate, lateral lobes subquadrate to suborbicular, the frontal margins abruptly contracted into a narrow central isthmus, the mid-lobe broadly dilated and 2-lobed, transversely reniform, occupying about ⅔ of the total length of the lip, the disk brown, with an erect, compact, 7-toothed basal callus. Column short, about 4 mm. long, with prominent lateral wings.

Costa Rica and Panama.

CANAL ZONE: San Juan, upper Chagres River, sea level, *Powell 397.* PANAMÁ: without definite locality, sea level, *Fairchild s. n.;* vicinity Pacora, sea level, *Allen 3442.* DARIÉN: Río Sambú, 200 m., *Pittier 5569.*

Robust lowland epiphytes, vegetatively nearly identical with *O. panamense* and *O. Baueri* but readily distinguished by the larger, conspicuously expanded mid-lobe and the much narrower isthmus of the lip.

14. Oncidium Kramerianum Rchb. f. in Otto & Dietr. Allgem. Gartenzeit. 23:9. 1855.

Oncidium Papilio var. *Kramerianum* Lindl. Folia Orch. Oncidium, (56). 1855.
Oncidium nodosum Ed. Morren in Belg. Hortic. 24:258. 1874, in adnot.
Papiliopsis nodosus Ed. Morren loc. cit. 1874.
Oncidium papilioniforme Regel, in Act. Hort. Petrop. 6:292. 1880.
Oncidium Kramerianum var. *resplendens* Rchb. f. in Gard. Chron. 3:360. 1888.

Erect, caespitose, epiphytic herbs with suborbicular to subquadrate, truncate, compressed, more or less rugose, monophyllous pseudobulbs 2.5–4 cm. in diameter, the bases enveloped in several papery, imbricating bracts which soon weather away. Leaves elliptic-oblong, acute, persistent, rigidly coriaceous, 15–25 cm. long and 3.5–6.5 cm. wide, contracted below into very short, conduplicate petioles, the lower surfaces of the leaves often more or less suffused with purple and with a strong central keel, the upper surfaces deep green, sometimes mottled darker green or purple. Inflorescences 1 or 2 erect or arching, prominently jointed scapes up to about 75 cm. in length, produced from the lateral bases of the pseudobulbs, the nodes conspicuously swollen, each provided with an elongate, acute, tubular, papery sheath clasping the lower halves of the cylindric internodes, the apex of the scape with a subconic, acute, terminal "bud" made up of several very closely imbricating sheaths, representing a much condensed raceme, the 5–8 flowers produced singly in succession from the axils of the sheaths, each flower lasting about a week. After the initially produced raceme has been exhausted, the scapes frequently elongate from one of the upper nodes, and again produce a series of flowers so that any given scape may remain in flower for as much as a year. Flowers large and richly colored. Sepals free, the dorsal sepal and the petals similar, erect, narrowly linear-spatulate, acute, rich reddish brown, the upper portions with undulate margins, 5.5–8 cm. long and 0.5–0.7 cm. wide, the lateral sepals very dissimilar, narrowly clawed at the base, the blades abruptly dilated above the claw, obliquely elliptic-ovate, obtuse to subacute, subfalcately deflexed with strongly undulate margins, yellow heavily blotched with rich reddish brown, 3–5 cm. long and 1–2.5 cm. wide. Lip about equaling the lateral sepals in length, subpandurate, 3-lobed, 3–4.5 cm. long and 3–4.5 cm. wide, richly blotched reddish brown, the lateral lobes rounded, the basal third of the lip suborbicular to transversely oblong in outline, undulate-margined, the central portion with a deep median constriction, which may sometimes be prolonged into a short, broad isthmus, the mid-lobe very large, spreading, transversely subquadrate to suborbicular, with a conspicuous bright yellow central blotch, the margins very strongly undulate, the disk at the base of the lip with a prominent, fleshy, minutely papillose, 5-parted, tuberculate crest. Column 6–8 mm. long, with 2 prominent lateral wings above which are 2 elongate, linear processes, thickened at the apices into small blackish glands.

Costa Rica to Colombia and Ecuador.

A very handsome species, often cultivated for its large, richly colored flowers. Although no authentic specimens have been collected in Panama, it has been several times reported from our area, notably from the vicinity of Chiriquí Lagoon and

from the vicinity of Puerto Armuelles. Since it is fairly frequent in closely adjacent territory in both Costa Rica and Colombia, there is every reason to believe that it will eventually be collected somewhere in the intermediate area.

15. ONCIDIUM NEBULOSUM Lindl. in Bot. Reg. n. s. 4: Misc. 175. 1841.

Oncidium Geertianum Morren, in Ann. Soc. Roy. d'Agr. et Bot. Gand 4:55, *t. 179*. 1848.
Oncidium caesium Rchb. f. in Gartenfl. 75. 1854.
Oncidium Klotzschianum Rchb. f. in Walp. Ann. 6:802. 1861.

Erect, epiphytic herbs with short, fleshy, approximate, ovoid to suborbicular, somewhat compressed, diphyllous pseudobulbs up to about 4 cm. long and 3 cm. wide, the bases usually with 2 foliaceous bracts. Leaves and bract blades narrowly lanceolate, obtuse to subacute, subcoriaceous, 9–20 cm. long and 2–2.5 cm. wide, contracted below into short, conduplicate petioles. Inflorescences 1 or 2 slender, erect or arching, few-flowered racemes up to about 36 cm. long, produced from the lateral bases of the pseudobulbs. Flowers relatively large, up to about 5 cm. long and 3 cm. wide. Sepals free, subequal, usually reflexed, pale yellow to greenish yellow, shaded or spotted with red or purple, lanceolate, acute, the lateral sepals somewhat oblique, 1.2–1.5 cm. long and 3–5.5 mm. wide. Petals spreading, subequal to the sepals or a little broader, ligular to elliptic-lanceolate, obtuse to subacute, yellow or greenish yellow, shaded or spotted with red or purple, 1.2–1.5 cm. long and 0.4–0.7 cm. wide. Lip pandurate, 3-lobed, 2–2.5 cm. long and 2–2.5 cm. wide, bright yellow, the lateral lobes small, obliquely triangular or subquadrate, obtuse, the anterior margins contracted into a narrow isthmus, the mid-lobe abruptly and broadly dilated and 2-lobed, transversely reniform, the disk with a short, fleshy, 5-toothed callus. Column about 5 mm. long, with prominent lateral wings.

Mexico, Guatemala, and Panama.

Absent from recent collections, but cited by Lindley (Fol. Orch. Oncidium (48). 1855) as "Wild in Veragua, Chiriqui, at 4–5000 ft.—Warczewicz." Probably a rather doubtful record, since it is not known from adjacent Costa Rica, or from any of the other Central American countries south of Guatemala.

16. ONCIDIUM OBRYZATUM Rchb. f. in Bonplandia 2:108. 1854.

Oncidium obryzatoides Kränzl. in Engler, Pflanzen. IV, Fam. 50 (Heft 80):240. 1922.
Oncidium fulgens Schltr. in Fedde Rep. Sp. Nov. Beih. 17:83. 1922.
Oncidium varians Schltr. loc. cit. 19:151. 1923.
Oncidium Brenesii Schltr. loc. cit. 257. 1923.
Oncidium graciliforme C. Schweinf. in Bot. Mus. Leafl. Harv. Univ. 5:96. 1938.

Erect, epiphytic herbs with approximate, suborbicular, ovoid, or elliptic-oblong, compressed, monophyllous pseudobulbs 2.5–9 cm. tall and 0.8–3 cm. wide, usually conspicuously ridged and wrinkled, often spotted or suffused with dark brown or black, the lower portions enveloped in the conduplicate, distichously imbricating bases of several bracts, the uppermost 2–4 of which are conspicuously foliaceous, the plants very variable in size, 1–4.5 dm. tall. Leaves and bract blades elliptic-oblong, ligular or sometimes narrowly linear, subacute, coriaceous, 10–35 cm. long

and 0.8–3.5 cm. wide, contracted below into slender conduplicate petioles. Inflorescences usually solitary, erect or arching, many-flowered panicles apparently always exceeding the leaves, in robust plants up to 1.5 m. in length, although often much less, in our specimens averaging about 4.5–6 dm. long. Flowers very variable in size, 1.5–3.5 cm. long and 1–2.5 cm. wide. Sepals subequal, free, spreading, obovate-spatulate, obtuse or truncate, golden yellow with chestnut-brown blotches at the base, 6–14 mm. long and 2.5–5 mm. wide. Petals usually broader than the sepals, obovate-spatulate, obtuse or truncate, golden yellow with basal chestnut-brown blotches, 6–12 mm. long and 3–6 mm. wide. Lip pandurate, 3-lobed, 10–20 mm. long and 8–20 mm. wide, golden yellow with a U-shaped reddish brown blotch surrounding the yellow basal callus, the lateral lobes subquadrate, obliquely triangular or rounded, the basal $\frac{2}{5}$ of the lip roughly triangular to suborbicular, the central portion of the lip abruptly contracted into a short, narrow isthmus, the mid-lobe dilated, spreading, 2-lobed with a deep central sinus, often transversely reniform in outline, the disk with an erect, fleshy basal crest, sometimes 5 (or more)-lobulate with 3 distinct apical teeth, or obscurely lobulate with only 2 distinct apical lobes. Column 3–4 mm. long, with prominent, usually porrect, lateral wings, the apices often more or less converging over the anther.

Costa Rica, Panama, Colombia, Ecuador, and Peru.

COCLÉ: region north of El Valle de Antón, 800–1000 m., *Allen 225, 2923, 2938, 3424.* CHIRIQUÍ: without definite locality, 4000–5000 ft., *Powell 3158, 3159, 3160, 3227;* vicinity Boquete, *Svihla s. n.*

A common, very variable species of the tree tops of areas of wet highland forest, distinguished from most other Panama Oncidiums by the obovate-spatulate, usually truncate sepals and petals.

17. ONCIDIUM OCHMATOCHILUM Rchb. f. in Bot. Zeit. 10:698. 1852.

Oncidium cardiochilum Lindl. Fol. Orch. Oncidium, (27). 1855.

Erect, usually robust, epiphytic herbs up to about 75 cm. tall, the many, conduplicate, distichously imbricating bases of the foliage contracted into a complanate petiole, often completely enveloping the usually inconspicuous, compressed, narrowly ovoid, diphyllous pseudobulb which may be up to about 10 cm. long and 2.5 cm. wide. Leaves narrowly lanceolate, acute to acuminate, coriaceous with prominent veins, sometimes conduplicate for their entire length, more frequently explanate, 25–70 cm. long and 1.5–6 cm. wide. Inflorescences 1 or 2 stout, erect or arching, many-flowered panicles up to about 2 m. in length but sometimes much shorter, produced from the axils of the uppermost basal leaves, the terminal portion of the inflorescence and the lateral branches distinctly flexiflex. Flowers of moderate size, averaging about 3 cm. long and 2 cm. wide when spread out, with a strong lilac-like fragrance when fresh. Sepals free, pale green marked with brown, the dorsal sepal lanceolate, acuminate, often strongly reflexed, 1.5–2 cm. long and 0.3–0.4 cm. wide, the lateral sepals obliquely linear-lanceolate, acuminate, the dorsal surface with a prominent central keel, 1.5–2 cm. long and

0.3–0.4 cm. wide. Petals broader than the sepals, elliptic-lanceolate, acute, brown or greenish brown, sometimes mottled white or with paler apices, 1.3–1.7 cm. long and 0.4–0.55 cm. wide. Lip panduriform, 3-lobed, 1–1.3 cm. long and 1–1.3 cm. wide, white spotted with brown or reddish purple at the base, the lateral lobes subquadrate, obtuse, projecting, the base of the lip subequal to, or sometimes exceeding the mid-lobe in width, the central portion contracted into a short distinct isthmus, the mid-lobe abruptly dilated, entire or apiculate, transversely semiorbicular or subcordate, the disk with a prominent, fleshy, multi-tuberculate callus terminating at the apex in a short, erect, obtuse, laterally compressed keel above and below which are 2 pairs of short fleshy teeth. Column 5–6 mm. long, apparently without lateral wings, the base without a foot.

Guatemala, Costa Rica, Panama, Colombia, Peru, and probably adjacent territories.

COCLÉ: El Valle de Antón, 3600 ft., *A. Bouché 9*. CHIRIQUÍ: without definite locality, 4500 ft., *Powell 160*.

The plant collected by Mr. Bouché was reported to have been a massive specimen weighing in the neighborhood of fifty pounds, with nearly a thousand flowers evidently borne on several inflorescences, the fragrance having been perceptible for some considerable distance.

18. ONCIDIUM PANAMENSE Schltr. in Fedde Rep. Sp. Nov. Beih. 17:85. 1922.

Erect, robust epiphytic herbs with approximate, oblong-ovoid, compressed, strongly ridged, diphyllous pseudobulbs 6–16 cm. long and 2–6 cm. wide, enveloped below in the conduplicate, distichously imbricating bases of 3–4 elongate, foliaceous bracts. Leaves and bract blades linear-lanceolate, acute, subcoriaceous, 12–75 cm. long and 1.5–4 cm. wide, contracted below into elongate, conduplicate petioles. Inflorescences 1 or 2 erect, arching, pendulous or sometimes scandent, many-flowered panicles 1–3.5 m. in length, produced from the lateral bases of the pseudobulbs. Flowers of moderate size averaging about 2.5 cm. in diameter. Sepals free, subequal, spreading, shortly clawed at the base, yellow heavily barred and blotched olive-brown, elliptic-obovate, acute, with somewhat undulate margins, 10–13 mm. long and 4–5 mm. wide. Petals subequal to the sepals and similarly colored, spreading, often with recurved apices, elliptic-obovate to elliptic-lanceolate, acute, with somewhat undulate margins, 10–12 mm. long and 4–5 mm. wide. Lip obscurely 3-lobed, broadly pandurate, yellow with a large, transverse, reddish brown to yellowish brown blotch below the crest, the lip 10–15 mm. long and 10–15 mm. wide, the lateral lobes rounded or broadly and obtusely triangular, the central lip with a sharp constriction but without a distinct isthmus, the mid-lobe emarginate, obscurely 2-lobed, transversely oblong or subreniform, the basal and apical halves of the lip of about equal width, the disk with an erect, white, fleshy crest surmounted by 4 divergent, usually crenulate keels, terminating at the apex in 3 distinct fleshy teeth. Column short, 3–5 mm. long, with 2 prominent, spreading, usually serrate, lateral wings.

Panama.

CANAL ZONE: San Juan, upper Chagres River, sea level, *Powell 416, 3201.* PANAMÁ: hills east of Panama City, sea level, *Powell 3228;* without definite locality, 50 m., *Kieswetter s. n.;* San José Island, Perlas Archipelago, *Erlanson 209;* vicinity Pacora, 25 m., *G. Fairchild s. n.;* vicinity Chepo, 20 m., *Allen 2360.*

A very common, robust, lowland species closely allied to the widely distributed Central American *O. sphacelatum,* but apparently differing in the broader basal callus and the larger column wings. Among the vegetatively similar or identical local species, it is separable from *O. isthmi* and *O. Baueri* by the uniformly broader basal half of the lip and the absence of a true isthmus, and from *O. ensatum* by the epiphytic habit and the presence of distinct articulations near the bases of the foliaceous bracts.

19. ONCIDIUM PANDURIFORME A. & S. in Sched. Orch. 8:77. 1925.

Erect, caespitose, epiphytic herbs 35–55 cm. tall, with distichous foliage, the conduplicate, imbricating bases enveloping a small, linear to narrowly ovoid, compressed, 1- or 2-leaved pseudobulb 5–7 cm. long and 0.8–2 cm. wide, the plants reminiscent of those of *Oncidium ochmatochilum.* Leaves linear-lanceolate, acute, subcoriaceous, rather coarsely veined, the blades up to about 40 cm. long and 1.5–3 cm. wide. Inflorescences usually solitary, stout, erect or arching, many-flowered panicles much exceeding the leaves, up to about 1 m. in length, produced from the axils of the foliaceous bracts, the terminal portion and the lateral branches usually distinctly fractiflex. Flowers rather small, averaging about 2 cm. in diameter. Sepals subequal, free, spreading or strongly reflexed, yellowish brown with yellow apices, the dorsal sepal lanceolate, acute, 9–12 mm. long and 2.5–3 mm. wide, the lateral sepals linear-lanceolate, acute, 10–12 mm. long and 2–2.5 mm. wide, the reverse surfaces with prominent central keels. Petals usually broader than the sepals, similarly colored, elliptic-lanceolate, acute, spreading or reflexed, 9–10 mm. long and 4–5 mm. wide. Lip pandurate, obscurely 3-lobed, white, 9–12 mm. long and 8–10 mm. wide, the lateral lobes small and rounded or obtusely triangular, the anterior margins converging to form a short, broad isthmus, the mid-lobe abruptly dilated, spreading, transversely semiorbicular, the under-surface at the apex with a short, strongly developed keel terminating in an apicule, the disk with a low, fleshy, obscurely tricarinate callus at the base. Column about 5 mm. long, without lateral wings but with 2 pronounced, parallel, marginal thickenings on the under-surface below the stigma.

Costa Rica and Panama.

CHIRIQUÍ: vicinity Bajo Chorro, headwaters of the Río Caldera, 1900 m., *Woodson & Schery 704.*

Apparently closely allied to *Oncidium ochmatochilum,* but differing in the obscure, lateral lobes of the lip, and the much less complexly developed basal callus.

20. ONCIDIUM PARVIFLORUM L. Wms. in Amer. Orchid Soc. Bull. 11:33. 1942.

Small, erect, epiphytic herbs, with approximate, elliptic-oblong, compressed, longitudinally ridged, monophyllous pseudobulbs 5–7 cm. long and 2–3 cm. wide,

densely spotted or suffused with brown, enveloped below in the conduplicate, distichously imbricating bases of several bracts, the uppermost 2 of which are conspicuously foliaceous. Leaves and bract blades ligular, obtuse, subcoriaceous,

Fig. 203. *Oncidium parviflorum*

11–13 cm. long and 1.2–1.6 cm. wide, contracted below into narrow, conduplicate petioles. Inflorescences solitary, erect or arching, many-flowered panicles up to about 75 cm. long, produced from the lateral bases of the pseudobulbs, the lateral branches very short, 1- to 3-flowered. Flowers small, 1.2–1.5 cm. in diameter. Sepals free, spreading, shortly clawed at the base, brown with yellow tips, the dorsal sepal elliptic-oblong, obtuse, shortly apiculate, 5–6 mm. long and about 3 mm. wide, the lateral sepals rather obliquely lanceolate, acute, with prominent dorsal keels, about 6 mm. long and 2.5 mm. wide. Petals clawed at the base, somewhat broader than the sepals, spreading, brown with yellow tips, oblong-ovate, obtuse, about 6 mm. long and 3.5 mm. wide. Lip pandurate, 3-lobed, 8–9 mm. long and 5–6 mm. wide, the frontal and lateral lobes yellow, the isthmus brown, the lateral lobes small, auriculate, with subacute deflexed apices, the central portion of the lip abruptly contracted into a broad isthmus, the mid-lobe emarginate and 2-lobed, subreniform, slightly exceeding the lateral lobes in width, the disk with a prominent, pubescent, 4-lobulate callus at the base, at first pure white, becoming yellow with age. Column about 3 mm. long, with 2 prominent lateral wings, which are rounded below and produced above into 2 erect, parallel, acuminate processes on either side of the anther.

Panama.

COCLÉ: region north of El Valle de Antón, about 1000 m., *Allen 2937*.

A small-flowered species, found in the tops of tall trees in the wet highland forests north of El Valle de Antón, in Coclé Province. Known only from the type collection.

21. ONCIDIUM POWELLII Schltr. in Fedde Rep. Sp. Nov. Beih. 17:86. 1922.

Erect, epiphytic herbs, with approximate, oblong-ovoid, compressed, longitudinally ridged, monophyllous pseudobulbs 6–13 cm. long and 2.5–5 cm. wide, partially enveloped below in the conduplicate, distichously imbricating bases of 3–4 foliaceous bracts. Leaves and bract blades oblong-lanceolate to ligular, usually obtuse or slightly retuse at the apex, or sometimes subacute, subcoriaceous, up to about 45 cm. in length but averaging about 20–25 cm. long and 2.5–5 cm. wide. Inflorescences usually solitary, arching, few- to many-flowered, flexuose panicles much exceeding the leaves, sometimes up to nearly 1.5 m. long but averaging about 7.5–9 dm., produced from the axils of the uppermost foliaceous bracts, each of the short lateral branches of the inflorescence with 1–3 flowers subtended by a few conspicuous, white, papery, spathaceous sheaths. Flowers variable in size but always large and attractive, 3–6 cm. in diameter. Sepals subequal, spreading, shortly clawed at the base, the blades with strongly undulate margins, rich chocolate-brown barred and margined yellow, the dorsal sepal free, erect, broadly elliptic-oblong to obovate, obtuse to subacute, 1.5–2.5 cm. long and about 1 cm. wide, the lateral sepals free or sometimes with the basal claws shortly connate, rather obliquely oblong, obtuse to subacute, 1.7–3 cm. long and 0.8–1.0 cm. wide.

Fig. 204. *Oncidium Powellii*

Petals spreading, with strongly undulate margins, subequal to the sepals or somewhat broader, the bases sessile, the blades rather obliquely oblong, obtuse to subacute, rich chocolate-brown with yellow margins and markings, 1.5–2.5 cm. long and 0.6–1.0 cm. wide. Lip pandurate, 3-lobed, shortly clawed at the base, 1.5–2 cm. long and 0.8–1.2 cm. wide, always distinctly shorter than the lateral sepals, the lateral lobes of the lip small, yellow, auriculate to subquadrate, truncate to subacute, the central portion of the lip contracted into a short, distinct, reddish brown isthmus, the mid-lobe bright yellow, quite variable in shape, usually shallowly emarginate, with a minute central apicule, the 2-lobed blade transversely reniform but sometimes only an obovate, obtuse, entire dilation of the isthmus, the disk with a prominent, yellow, multidenticulate callus, terminating at the apex in a broad, transverse, porrect, more or less verrucose or crenulate plate. Column 5–6 mm. long, without conspicuous lateral wings.

Panama.

CANAL ZONE: Gatún Lake, sea level, *Powell 58*; without definite locality, *Pring s. n.*; hills near Frijoles, sea level, *Powell 3480*. COCLÉ: vicinity of El Valle de Antón, 800 m., *Allen 2895*.

An apparently rare species, with very handsome chocolate-brown flowers, seemingly confined to the lowland forests of the Atlantic slope. It is very closely allied to the Colombian *O. anthocrene*, and may ultimately prove to be identical.

22. ONCIDIUM PUSILLUM (L.) Rchb. f. in Walp. Ann. 6:714. 1863.

Epidendrum pusillum L. Sp. Pl. ed. 2, 1352. 1763.
Cymbidium pusillum Sw. in Nov. Act. Soc. Upsal. 6:74. 1799.
Oncidium iridifolium HBK. Nov. Gen. & Sp. 1:344. 1815.

Dwarf, epiphytic herbs up to about 8 cm. tall, entirely without pseudobulbs. Leaves distichously spreading, forming a broad fan, equitant, linear, often falcate or ensiform, the apices obliquely acute, 2–6 cm. long and 0.4–1.0 cm. wide. Inflorescences 1 to about 6 erect or arching scapes, about equaling the leaves in length, the apices with several acute, strongly compressed, imbricating sheaths, forming a short, complanate raceme from the axils of which the flowers are produced in succession. Flowers large in relation to the size of the plant, averaging 2–2.5 cm. long and 1.8–2 cm. wide. Sepals free, spreading, bright yellow, the dorsal sepal erect, elliptic-lanceolate to subquadrate, obtuse, up to about 5 mm. long and 3–4 mm. wide, the dorsal surface with a pronounced keel, prolonged at the apex into an erect, acute spur, the lateral sepals linear-lanceolate, acuminate, very closely appressed to the under-surface of the lip, 4–5 mm. long and 1–1.5 mm. wide, the reverse surfaces with a strongly developed keel. Petals spreading, oblong, obtuse, with undulate margins, bright yellow irregularly barred with reddish brown, up to about 8 mm. long and 4 mm. wide. Lip broadly pandurate, 3-lobed, up to 1.8 cm. long and 2 cm. wide, bright yellow, the lateral lobes suborbicular to obovate-spatulate, obtuse, spreading, the central portion of the lip contracted into a short, broad isthmus, blotched with reddish brown, the mid-lobe

Fig. 205. *Oncidium pusillum*

abruptly dilated, with a deep central sinus, the lateral lobules broadly spreading, with undulate margins, the disk white, spotted reddish orange, with a spreading, subquadrate plate, terminating in a second broad, spreading, semi-orbicular plate with a short central keel and undulate margins. Column short, about 3 mm. long, with prominent, denticulate, lateral wings.

Mexico to Brazil and Bolivia; Trinidad.

CANAL ZONE: Las Cascadas Plantation, near Summit, *Standley 25761*, *Powell 3018;* San Juan, upper Chagres River, sea level, *Powell 3346;* drowned forest along the Río Chagres, upper Madden Lake area, *Steyermark & Allen 16771;* vicinity Salamanca Hydrographic Station, 80 m., *Woodson, Allen & Seibert 1559;* vicinity Alajuela, 90–100 m., Madden Dam area, *Dodge, Steyermark & Allen 16510.* PANAMÁ: Río La Maestra, between the Río Bayano and the Gulf of San Miguel, 0–25 m., *Allen 17.* BOCAS DEL TORO: Water Valley, vicinity Chiriquí Lagoon, *von Wedel 1383, 1474, 1482, 2153;* Western River, vicinity Chiriquí Lagoon, *von Wedel 2777;* Almirante Bay, *von Wedel 14.*

Attractive plants, with relatively large, bright yellow flowers, often found as colonies on old orange trees or scattered through the slender, twiggy ends of dead branches, often overhanging water. Widely distributed and common in the American tropics.

23. ONCIDIUM STENOTIS Rchb. f. in Linnaea 41:67. 1877.

Erect, epiphytic herbs with approximate, linear-oblong, compressed, longitudinally ridged, monophyllous pseudobulbs 7–14 cm. long and 2.5–4 cm. wide, the lower portions enveloped in the conduplicate, distichously imbricating bases of several bracts the uppermost 3 of which are conspicuously foliaceous. Leaves and bract blades linear-oblong, obtuse to subacute, coriaceous, 15–60 cm. long and 2.5–5 cm. wide, contracted below into very short, conduplicate petioles. Inflorescences 1 or 2 erect or arching, few- to many-flowered panicles up to about

1.5 m. in length, the lateral branches short, usually less than 15 cm. long, the 1 to 5 flowers subtended by thin, white, acuminate, papery bracts. Flowers of moderate size, 3–4 cm. in diameter. Sepals free, subequal, spreading, with recurved apices and undulate margins, yellow heavily blotched with brown, the dorsal sepal oblong-lanceolate, shortly acute to apiculate, 1.3–1.8 cm. long and 0.6–0.8 cm. wide, the lateral sepals linear-lanceolate to lanceolate, acute, obliquely deflexed, the reverse surfaces with a strong central keel, 1.5–2 cm. long and 0.5–0.7 cm. wide. Petals subequal to the sepals and similarly colored, spreading, with recurved apices and undulate margins, lanceolate, acute, 1.4–1.6 cm. long and 0.4–0.6 cm. wide. Lip pandurate, 3-lobed, distinctly shorter than the lateral sepals, 1.2–2 cm. long and 1.2–1.8 cm. wide, bright yellow with a brown isthmus, the lateral lobes shortly clawed at the base, spreading, obovate-spatulate, with subquadrate to suborbicular blades, the central portion of the lip contracted into a narrow isthmus, the mid-lobe abruptly dilated, emarginate and 2-lobed, often with a short central apicule, transversely subreniform in outline, about equaling the extended lateral lobes in width, the disk with an erect, fleshy callus, the sides with 2 or 3 short teeth, the apex abruptly tridenticulate. Column up to about 7 mm. long, with 2 rather obscure lateral lobes, the under-surface below the stigma conspicuously thickened into 2 parallel, fleshy lobules.

Costa Rica and Panama.

CHIRIQUÍ: without definite locality, *Pring s. n.*, *Pring & Hunter s. n.* BOCAS DEL TORO: Water Valley, vicinity Chiriquí Lagoon, *von Wedel 1654, 1829, 2156.*

Allied to *O. Baueri,* but apparently always differing in the larger flowers, in which the lip is distinctly shorter than the lateral sepals, and with a conspicuously narrower isthmus. The smaller plants are nearly identical in vegetative appearance with those of *O. Powellii,* and have sometimes been mistaken for that species.

24. ONCIDIUM STIPITATUM Lindl. in Bot. Voy. Sulphur, 172. 1843.

Oncidium lacerum Lindl. in Bot. Reg. n. s. 7: Misc. 30. 1844.
Oncidium stipitatum Lindl. var. *platyonyx* Rchb. f. in Gard. Chron. 1:788. 1878.

Caespitose, epiphytic herbs with very short, subcylindric to subconic, monophyllous pseudobulbs 5–10 mm. long and 5–10 mm. wide, the broadly truncate apices with elongate, fleshy, terete, acuminate, longitudinally sulcate leaves, the pseudobulbs and leaf bases of the current season's growth enveloped in 4–6 closely imbricating, papery bracts which soon weather away. Leaves at first horizontal or ascending, becoming pendulous and wrinkled with age, often more or less spotted with reddish brown, 24–70 cm. long and 0.6–1.0 cm. in diameter. Inflorescences solitary, horizontal or ascending, many-flowered panicles usually about equaling the leaves in length, produced from the bases of the pseudobulbs. Flowers very variable in size, up to about 2.5 cm. long and 1.8 cm. wide, always brightly colored and attractive. Sepals subequal, free, spreading, shortly clawed at the base, yellow richly marked with reddish brown, the dorsal sepal obovate-spatulate, obtuse with a minute apicule, the blade slightly concave, 4.5–6 mm.

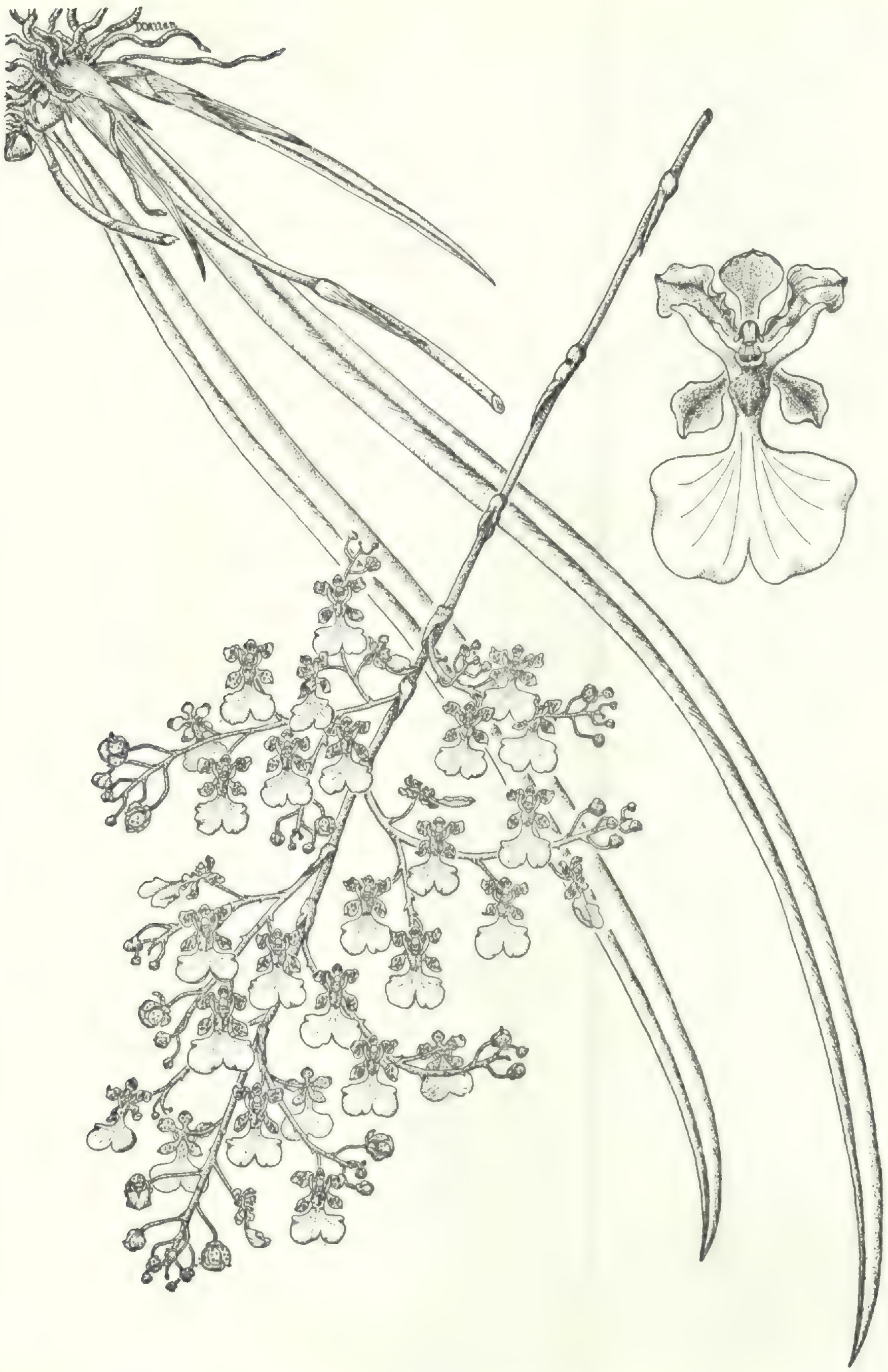


Fig. 206. *Oncidium stipitatum*

long and 2.5–4 mm. wide, the lateral sepals obliquely obovate, shortly acute, 5–7 mm. long and 3–4 mm. wide. Petals spreading, elliptic-oblong, obtuse, with undulate margins, colored and marked similarly to the sepals, 5–8 mm. long and 2–3 mm. wide. Lip pandurate, 3-lobed, 1–2 cm. long and 1–1.8 cm. wide, bright yellow on both the frontal and reverse surfaces, the basal half of the isthmus reddish brown, the lateral lobes linear-oblong, obliquely obtuse, spreading or ascending, the central portion of the lip contracted into a narrow isthmus, the mid-lobe abruptly dilated and 2-lobed, transversely semiorbicular to oblong, often with undulate margins, the disk at the base with a suborbicular transverse plate terminating at the apex in a prominent, erect, fleshy, semiorbicular, somewhat laterally compressed tubercle occupying only the basal half of the isthmus. Column 2–2.5 mm. long, with 2 narrow, spreading, lateral arms.

Panama.

CANAL ZONE: vicinity of Empire and Culebra Cut, 80 m., *Hunter & Allen 784;* Miraflores, sea level, *Powell 3207;* Las Cruces, *Powell 3222;* Las Cascadas, *Powell 3124;* Barro Colorado Island, Gatún Lake, *Woodworth & Vestal 529;* San Juan, upper Chagres River, 0–200 ft., *Powell 3137.* COLÓN: forests along the Río Boquerón, above the Peluca Hydrographic Station, Upper Madden Lake region, 90 m., *Hunter & Allen 654.* PANAMÁ: hills near Panama City and near Tapía, sea level, *Powell 220, 375;* vicinity Arraiján, *Powell 3209;* Chilibre River, *Piper s. n.;* coastal swamp along the Río Jagua, east of Panama City, sea level, *Hunter & Allen 472;* Cerro Campana, vicinity Campana, 2000 ft., *Fairchild s. n., Allen 4488;* vicinity Pacora, about 50 m., *Allen 810, 2033, 4451, 4457;* vicinity La Chorrera, 50 ft., *Allen 5168.*

A very common, attractive lowland species apparently confined to the central Isthmian area, particularly on the Pacific slope, where the plants are very abundant in areas of deciduous forest, with spontaneous seedlings often spreading to cultivated trees and shrubs of the Canal Zone town sites.

25. ONCIDIUM TERES A. & S. in Sched. Orch. 8:78, *t. 7.* 1925.

Epiphytic herbs with slender, fleshy, terete, longitudinally sulcate leaves. Inflorescences paniculate, many-flowered, up to about 4.5 dm. long, produced from the bases of the rudimentary, subcylindric pseudobulbs. Flowers small, up to about 1.5 cm. long and 1 cm. wide. Sepals free, subequal, spreading, shortly clawed at the base, obovate-spatulate, the blades suborbicular, obtuse, concave, minutely apiculate, yellow very heavily spotted reddish brown, about 6 mm. long and 3.5–4.5 mm. wide. Petals spreading, marked and colored similarly to the sepals, oblong-obovate, obtuse, with undulate margins, 5.2–6 mm. long and 3–4 mm. wide. Lip panduriform, 3-lobed, 7–8 mm. long and 6.5–8 mm. wide, the frontal surface bright yellow, the reverse surface and the disk heavily spotted reddish brown, the lateral lobes small, ligular or oblong-spatulate, obtuse to obliquely acute, minutely puberulent, antrorse in natural position, the central portion of the lip contracted into a distinct isthmus, the mid-lobe abruptly dilated, obscurely 2-lobed, transversely reniform, sometimes porrect in natural position, the disk with

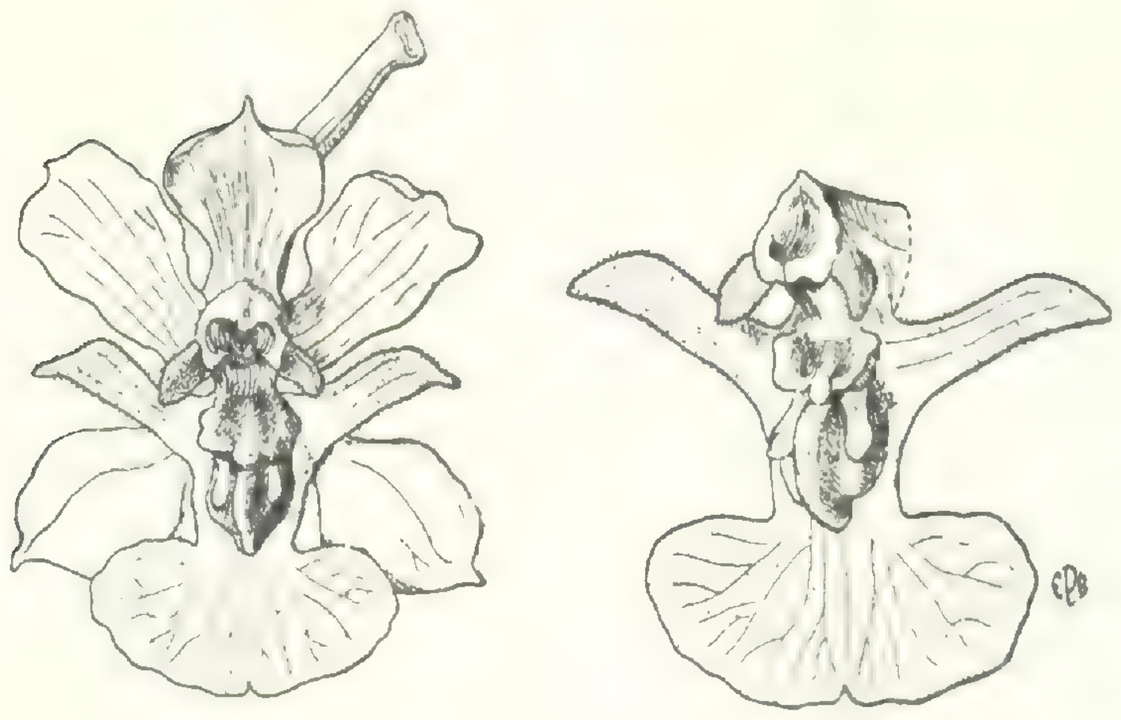


Fig. 207. *Oncidium teres*

a prominent, complex, fleshy, tuberculate callus, occupying nearly the entire isthmus. Column about 3 mm. long, with 2 lateral, acute, incurving wings.

Panama.

VERAGUAS: vicinity San Francisco de Veraguas, 1000 ft., *Powell 383*. CHIRIQUÍ: vicinity David, 100 ft., *Allen 4242, 4453*.

A small-flowered lowland species thus far known only from Chiriquí and Veraguas provinces in western Panama. The plants are vegetatively identical with those of *Oncidium stipitatum*, but the flowers differ in the shorter isthmus of the lip, the much more prominent and complex basal callus, the reddish brown spotting on the reverse surface of the lip, and in other characters.

26. ONCIDIUM WARSCEWICZII Rchb. f. in Bot. Zeit. 10:693. 1852.

Oncidium bifrons Lindl. in Gard. Chron. 84. 1857.

Erect, caespitose, epiphytic herbs with approximate, elliptic-ovoid, compressed, usually diphyllous pseudobulbs 4–8 cm. tall and 2–3 cm. wide, the bases enveloped in several conduplicate, imbricating bracts, the uppermost bract being conspicuously foliaceous. Leaves ligular, obtuse to subacute, subcoriaceous, 15–30 cm. long and 1.5–3.5 cm. wide, contracted below into slender, conduplicate petioles. Inflorescence a solitary, erect or arching, 4- to 12-flowered, unilateral raceme exceeding the leaves, up to about 5 dm. long, produced from the axil of the uppermost foliaceous bract. Flowers of moderate size, about 3 cm. in diameter, uniformly yellow throughout, the elongate pedicels subtended by conspicuous, papery, spathaceous bracts. Sepals dissimilar, the dorsal sepal free, oblong, obtuse, with slightly undulate margins, 10–12 mm. long and 5–6 mm. wide, the lateral sepals connate nearly to the apex, forming a single obovate, bifid segment below the lip, the lower surface with 2 distinct keels, 1.4–1.6 cm. long and 0.7–0.9 cm. wide. Petals obliquely oblong, obtuse, with slightly undulate margins, 1.2–1.4 cm. long and 0.7–0.8 cm. wide. Lip subpandurate, obscurely 3-lobed, 1.5–1.8 cm. long and 1.5–1.8 cm. wide at the apex, the lateral lobes reduced to inconspicuous auricles, the basal half of the lip nearly oblong, the apical half abruptly dilated and 2-lobed, reniform, about twice as wide as the basal half, the disk with a nar-

row, fleshy crest, the base under the column semiterete, terminating at the apex in 5 short, divergent teeth. Column 8–10 mm. long, the apex dilated, with narrow lateral wings.

Costa Rica and Panama.

Originally described from plants collected by von Warscewicz, presumably on the slopes of Chiriquí Volcano, at 8000–10,000 ft. elevation. Although the species is not represented in recent collections from our area, its frequent occurrence in the adjacent Costa Rican highlands would lend weight to the supposition that this one citation may be authentic.

DOUBTFUL SPECIES

ONCIDIUM ADVENA Rchb. f. in Hamb. Gartenzeit. 16:422. 1860.

Originally described from flowering material only, from plants presumably imported from Venezuela. An Endres collection is cited by Kränzlin, from the vicinity of the old Obispo railway station, in the Canal Zone. The figure given of a single flower looks like *Oncidium ensatum*. Absent from all recent collections.

ONCIDIUM ONUSTUM Lindl. Gen. & Sp. Orch. Pl. 203. 1833.

A poorly known South American species, sometimes doubtfully listed as occurring in Panama. Absent from all recent collections.

ONCIDIUM PELIOGRAMA Linden & Rchb. f. in Gard. Chron. 1451. 1871.

Described from flowers only. On the basis of the sketch of the type in the Ames Herbarium, the species which we list as *Oncidium stenotis* might possibly be referable to this concept, but the drawing is too poor for positive identification. In the absence of authentic material for comparison, or even any description of vegetative parts, it seems best to exclude it as a species of doubtful identity.

79. LEOCHILUS Knowles & Westcott

LEOCHILUS Knowles & Westc. Fl. Cab. 2:143. 1838; Benth. & Hook. Gen. Pl. 3:564. 1883; Kränzl. in Engler, Pflanzenr. IV, Fam. 50 (Heft 80):291. 1922.

Cryptosanus Scheidw. in Otto & Dietr. Allg. Gartenzeit. 11:101. 1843.
Rhynchostele Rchb. f. in Bot. Zeit. 10:770. 1852.
Cryptosaccus Scheidw. ex Rchb. f. Xenia Orch. 1:15. 1854.
Leiochilus Benth. in Jour. Linn. Soc. 18:328. 1881, non Hook.
Waluewa Regel, in Gartenfl. 40:89, *t. 1341*. 1891.
Rhynchostelis Jackson, in Index Kew. 2:718. 1895, sphalm.

Small, caespitose, epiphytic herbs with short, compressed, monophyllous or rarely diphyllous pseudobulbs, the lower portions enveloped in several membranaceous or foliaceous sheaths. Leaves elliptic-lanceolate to ligular, coriaceous, contracted below into a petiole. Inflorescences 1 or 2 erect or arching racemes or panicles produced from the lateral bases of the pseudobulbs. Flowers small. Sepals subequal, spreading, free, or more or less connate. Petals subequal to the sepals or sometimes broader. Lip entire or 3-lobed, adnate to the base of the

column, spreading, usually longer than the lateral sepals, the disk fleshy or callous. Column short, erect, not laterally winged but usually biauriculate below the stigma, the clinandrium truncate, the rostellum elongate, the base of the column without a foot. Anther terminal, operculate, incumbent, 1-celled, produced in front into a hooded appendage; pollinia 2, waxy.

A small genus of tropical American epiphytes closely allied to *Oncidium*, ranging from Mexico and the West Indies to northern Argentina. Two species are known from Panama.

a. Lateral sepals connate for more than half their length..... 1. L. LABIATUS
aa. Lateral sepals free..... 2. L. SCRIPTUS

1. LEOCHILUS LABIATUS (Sw.) O. Ktze. Rev. Gen. Pl. 2:656. 1891 (as *Leiochilus*).

Epidendrum labiatum Sw. Prodr. Veg. Ind. Occ. 124. 1788.
Liparis labiata Spr. Syst. Veg. 3:741. 1826.
Rodriguezia cochlearis Lindl. in Ann. & Mag. Nat. Hist. 5:116. 1840.
Leochilus cochlearis Lindl. in Bot. Reg. n. s. 5: Misc. 23. 1842.
Oncidium labiatum Rchb. f. in Walp. Ann. 6:741. 1863.

Dwarf, epiphytic herbs 4–9 cm. tall, with elliptic oblong, compressed, monophyllous pseudobulbs 10–15 mm. long and 5–8 mm. wide, the bases with 2–3 foliaceous bracts, the leaves and pseudobulbs often reddish brown. Leaves and bract blades elliptic-lanceolate to ligular, obtuse to subacute, coriaceous, 2–6 cm. long and 0.6–1.5 cm. wide. Inflorescences 1 or 2 slender, erect, few-flowered racemes or shortly branching panicles much exceeding the leaves in length, 4–25 cm. long. Flowers small, averaging about 1 cm. in diameter. Sepals of about equal length, yellow striped or spotted reddish brown, the dorsal sepal free, elliptic-lanceolate, shortly acuminate, deeply concave, 3–5 mm. long and 1.5–2 mm. wide, the lateral sepals connate to above the middle, forming a single bifid segment below the lip, 4–6 mm. long and 2.5–3 mm. wide, with 2 distinct keels on the lower surface. Petals subequal to the dorsal sepal and similarly colored, elliptic-oblong, subacute, with distinct central keels on the reverse surfaces, 3–5 mm. long and 2–3 mm. wide. Lip entire, slightly concave, yellow with a red or reddish brown spot at the base, oblanceolate, obtuse or sometimes slightly retuse, the blade with an obscure median constriction, 5–8 mm. long and 2.5–4 mm. wide, the disk with an erect, bicarinate, fleshy callus. Column 1–1.5 mm. long, semiterete, without lateral wings but with 2 short, porrect teeth below the stigma.

Antilles, Panama, and Trinidad.

COCLÉ: El Valle de Antón, 800 m., *Allen 2295*.

A dwarf species, fairly frequent on calabash trees in cultivated plots, the plants being rendered conspicuous by the reddish brown leaves and pseudobulbs. Our specimens are nearly identical with typical West Indian material, but differ considerably from specimens of *Leochilus gracilis* Schltr. from Guatemala, Honduras, and Costa Rica, which would seem to be distinct. In *L. labiatus* the plants are

from 4–9 cm. in height, with elongate scapes up to 25 cm. long, the flowers averaging slightly larger, with the lateral sepals connate to above the middle; while in *L. gracilis* the plants seem to be 2–4.5 cm. tall, the scapes only up to about 6 cm. long, with the lateral sepals entirely free.

2. LEOCHILUS SCRIPTUS (Scheidw.) Rchb. f. Xenia Orch. 1:15, *t. 6.* 1854.

Cryptosanus scriptus Scheidw. in Otto & Dietr. Allg. Gartenzeit. 11:101. 1843.
Oncidium scriptum Rchb. f. in Walp. Ann. 6:772. 1863.
Leochilus major Schltr. in Fedde Rep. Sp. Nov. 15:209. 1918.
Leochilus Powellii Schltr. loc. cit. 17:81. 1922.
Leiochilus retusus Schltr. loc. cit. 19:256. 1923.

Erect, caespitose, epiphytic herbs with approximate, oblong-ovoid to elliptic-oblong, compressed pseudobulbs 2–5 cm. long and 1–2.5 cm. wide, the truncate apices usually monophyllous, the lower portions of the pseudobulbs enveloped in the conduplicate bases of the several distichously imbricating bracts the uppermost 2 or 3 of which are conspicuously foliaceous. Leaves ligular, obtuse or shortly and unequally 2-lobed at the apex, coriaceous, 5.5–14 cm. long and 1–2.8 cm. wide, contracted below into very short, conduplicate petioles. Inflorescences 1 or 2 erect or arching, few- to about 12-flowered racemes or weakly branching panicles, equaling or somewhat exceeding the leaves, up to about 25 cm. in length. Flowers relatively large for the genus, averaging about 1.5–2 cm. in diameter, greenish white to greenish yellow with purple or reddish brown markings. Sepals free, subequal, spreading, the dorsal sepal elliptic-lanceolate, acute, somewhat concave, the reverse surface with a distinct keel, 9–12 mm. long and 3.5–5 mm. wide, the lateral sepals spreading or somewhat reflexed, ligular to oblong-lanceolate, obtuse to subacute, 8–12 mm. long and 2.5–5 mm. wide, the reverse surfaces with a distinct central keel. Petals subequal to the dorsal sepal, lanceolate, acute, 9–12 mm. long and 2.5–3.5 mm. wide. Lip entire, spreading or slightly convex, the blade obovate-oblong, truncate, up to about 12 mm. long and 7 mm. wide, the narrower base conspicuously thickened and adnate to the base of the column, the broader apex shallowly emarginate, the reverse surface with a distinct central keel, the disk with a short, subquadrate, basal boss terminating at the apex in 2 distinct, parallel, erect, fleshy, puberulent calli. Column up to about 3 mm. long, semiterete, the under-surface below the stigma with 2 distinct, ligular, porrect arms.

Guatemala, Honduras, Costa Rica, and Panama.

CANAL ZONE: Las Cascadas, sea level, *Powell 3140, Standley 25755, 29700;* vicinity Gatún, *H. Butcher s.n.* PANAMÁ: Juan Díaz Range, sea level, *Powell 129;* Arraiján, *Powell 3128, 3206;* Río La Maestra, 0–25 m., *Allen 50;* vicinity Chepo, 30 m., *Allen 2355.*

80. SIGMATOSTALIX Rchb. f.

SIGMATOSTALIX Rchb. f. in Bot. Zeit. 10:769. 1852; Benth. & Hook. Gen. Pl. 3:565. 1883; Schltr. in Fedde Rep. Sp. Nov. 15:142. 1918.

Ornithophora Barb. Rodr. Gen. & Spec. Orch. Nov. 2:225. 1882.

Small, caespitose, epiphytic herbs with approximate, elliptic-oblong to ovoid, compressed, monophyllous or rarely diphyllous pseudobulbs, the lower portions partially enveloped in several distichously imbricating bracts the uppermost 2 to 5 of which are usually foliaceous. Leaves linear to elliptic-lanceolate, subcoriaceous to coriaceous. Inflorescences 1 to about 5 erect or arching, few- to many-flowered racemes or panicles about equaling or sometimes much exceeding the leaves in length, produced from the axils of the foliaceous bracts. Flowers small to minute. Sepals subequal, free, or with the laterals shortly connate at the base. Petals subequal to the sepals. Lip usually with an elongate claw, sometimes subsessile, the blade entire or 3-lobed, subquadrate, suborbicular or trulliform. Column slender, elongate, often somewhat arcuate, the apex more or less dilated opposite the stigma. Anther terminal, operculate, incumbent, 1-celled; pollinia 2, waxy.

A small genus of tropical American epiphytes, ranging from Mexico to Brazil. Four species are known to occur in Panama.

a. Lip subsessile, without an elongate claw at the base.
  b. Basal callus of the lip subquadrate, with a deep longitudinal excision on each side of the central concavity ..... 4. S. RACEMIFERA
  bb. Basal callus of the lip transversely subreniform, bifid, with a rounded tubercle in the center of each of the lateral lobules ..... 3. S. HYMENANTHA
aa. Lip with a distinct, elongate claw at the base.
  b. Blade of the lip subquadrate, without distinct auriculate lobules at the base ..... 1. S. ABORTIVA
  bb. Blade of the lip ovate-sagittate to cordate, with 2 distinct auriculate lobules at the base ..... 2. S. GUATEMALENSIS

1. SIGMATOSTALIX ABORTIVA L. Wms. in Ann. Mo. Bot. Gard. 27:284, *t. 34, figs. 1–6.* 1940.

Dwarf, caespitose, epiphytic herbs, with oblong-elliptic, compressed, monophyllous pseudobulbs 12–20 mm. long and 3–11 mm. wide, enveloped below in the conduplicate, distichously imbricating bases of 2 foliaceous bracts. Leaves and bract blades narrowly linear-ligular to elliptic-lanceolate, acute, subcoriaceous, 2–4 cm. long and 0.5–1.0 cm. wide, contracted below into very short, conduplicate petioles. Inflorescences usually solitary, slender, arching, few-flowered racemes up to about 10 cm. long. Flowers minute, averaging about 5 mm. in length. Sepals subequal, free, spreading or reflexed, yellow, lanceolate, acute, about 3.2 mm. long and 0.8–1 mm. wide. Petals somewhat broader than the sepals, yellow, elliptic-lanceolate to oblanceolate, subacute and obscurely apiculate, about 3.2 mm. long and 1.3 mm. wide. Lip with an elongate claw at the base, obovate-spatulate, white, about 5 mm. long and 3.5 mm. wide, the abruptly dilated blade truncate at the apex, subquadrate to suborbicular in outline, the disk with a fleshy, cucullate callus covering the entire upper surface of the claw, the obtuse apex abruptly erect. Column slender, about 3 mm. long, dilated at the apex.

Panama.

COLÓN: Quebrada Lopez, lower slopes of Cerro Santa Rita, 30 m., *Allen 2121.*

Fig. 208. *Sigmatostalix guatemalensis*

2. SIGMATOSTALIX GUATEMALENSIS Schltr. in Fedde Rep. Sp. Nov. 10:253. 1911.

Sigmatostalix costaricensis Rolfe in Kew Bull. 78. 1916; Bot. Mag. *t. 8825.* 1919.
Sigmatostalix poikilostalix Kränzl. in Engler, Pflanzenr. IV, Fam. 50 (Heft 80):310, *fig. 27, D:a-e.* 1922.

Caespitose, epiphytic herbs with approximate, elliptic-oblong, compressed, monophyllous pseudobulbs 1.5–3.5 cm. long and 0.6–1.5 cm. wide, partially enveloped below in the conduplicate bases of several distichously imbricating bracts the uppermost 2 or 3 of which are conspicuously foliaceous. Leaves and bract blades ligular to elliptic-lanceolate, acute, subcoriaceous, 3.5–12 cm. long and 0.8–1.5 cm. wide, contracted below into short, conduplicate petioles. Inflorescences 1 or 2 slender, erect, few- to many-flowered racemes, usually much exceeding the leaves in length, 11–32 cm. long, produced from the axils of the uppermost foliaceous bracts. Flowers relatively large for the genus, averaging about 12–15 mm. in diameter when spread out. Sepals free, subequal, usually strongly reflexed, pale green to yellow, usually marked with brown, ligular-lanceolate, acute, 6–9 mm. long and 1.5–2.5 mm. wide. Petals subequal to the sepals and similarly colored, usually strongly reflexed, rather obliquely lanceolate, acute, 6–9 mm. long and 2–3 mm. wide. Lip with a distinct, narrow, fleshy claw at the base, 2–3 mm. long, produced in front into a short, subacute spur, the blade of the lip abruptly dilated, rather obscurely 3-lobed, spreading or slightly convex, broadly trulliform, ovate-sagittate to cordate, usually reddish brown with a dark yellow apex, rarely entirely yellow, 5–6 mm. long and 4–5 mm. broad, the lateral lobules small, auriculate or with subfalcately acute, incurving projections from the posterior margin, the apex of the blade obtuse to acute, with a short, distinct, central keel on the under-side. Column elongate, slender, somewhat arcuate, up to about 6 mm. long, the lower portion terete, the apex shortly dilated on either side of the stigma, the base without a foot.

Mexico, Guatemala, Costa Rica, and Panama.

CHIRIQUÍ: without definite locality, 5000 ft., *Powell 230.*

3. SIGMATOSTALIX HYMENANTHA Schltr. in Beih. Bot. Centralbl. 36^2:419. 1918.

Small, caespitose, epiphytic herbs with approximate, ovoid to elliptic-oblong, compressed, monophyllous pseudobulbs 1.2–3.5 cm. long and 0.8–2 cm. wide, the lower portions partially enveloped in the conduplicate, distichously imbricating bases of several bracts, the uppermost 2 or 3 of which are conspicuously foliaceous. Leaves and bract blades linear-ligular, acute, subcoriaceous, 3.5–14 cm. long and 0.4–0.8 cm. wide, contracted below into narrow, conduplicate petioles. Inflorescences 1 or 2 slender, erect, shortly branching panicles, usually about equaling the leaves in length, produced from the axils of the uppermost foliaceous bracts, the lateral branches of the panicles usually very short and densely bracteate. Flowers minute. Sepals and petals oblong, acute, about 2 mm. long and 0.5 mm. wide. Lip obscurely 3-lobed, about 1.5 mm. long and 2 mm. wide, subsessile or obscurely

clawed at the base, the blade broadly ovate, obtuse, spreading or slightly convex, the disk with a fleshy, 2-lobed, transversely subreniform callus, with an obscure, rounded tubercle in the center of each of the lateral lobules. Column stout, terete, erect, slightly dilated at the apex, about 1.5 mm. long, the base without a foot.

Costa Rica and Panama.

DARIÉN: vicinity Chepigana, Cana-Cuasi trail, 2000 ft., *Terry & Terry 1437*.

4. SIGMATOSTALIX RACEMIFERA L. Wms. in Ann. Mo. Bot. Gard. 27:285, *t. 36*. 1940.

Small, caespitose, epiphytic herbs 7–15 cm. tall, with elliptic-oblong, compressed, monophyllous pseudobulbs 2–3.5 cm. long and 1–2 cm. wide, the lower portions enveloped in the conduplicate, distichously imbricating bases of several bracts, the uppermost 3 to 5 of which are conspicuously foliaceous. Leaves and bract blades linear-ligular to elliptic-lanceolate, acute, subcoriaceous, 3–13 cm. long and 0.5–1.8 cm. wide, contracted below into short, conduplicate petioles. Inflorescences 1 to 5, slender, erect or arching, few- to many-flowered, shortly branching panicles about equaling or somewhat exceeding the leaves in length, produced from the axils of the foliaceous bracts. Flowers small. Sepals subequal, spreading or reflexed, greenish white, the dorsal sepal free, lanceolate, acute, about 3 mm. long and 0.75 mm. wide, the lateral sepals shortly connate at the base, elliptic-lanceolate, acute to shortly acuminate, about 2.5 mm. long and 0.8 mm. wide. Petals somewhat broader than the sepals, greenish-white spotted maroon, elliptic-lanceolate, acute, about 3 mm. long and 1.25 mm. wide. Lip subsessile or obscurely clawed at the base, the blade subquadrate, truncate, with a distinct median constriction, orange, about 3 mm. long and 3.5 mm. wide, the disk with a fleshy, subquadrate callus, with a deep longitudinal excision on each side of the central linear concavity. Column elongate, slender, about 5 mm. long, terete below, dilated above, with 2 acute auricles on each side of the stigma.

Panama.

COCLÉ: hills north of El Valle de Antón, 800–1000 m., *Allen 1232, 2266, 2744, 2878, 3745*.

81. LOCKHARTIA Hook.

LOCKHARTIA Hook. in Bot. Mag. *t. 2715*. 1827; Benth. & Hook. Gen. Pl. 3:570. 1883; Kränzl. in Engler, Pflanzenr. IV, Fam. 50 (Heft 83):6. 1923.

Fernandezia R. & P., sensu Lindl. Gen. & Sp. Orch. Pl. 207. 1833, in part.

Caespitose, epiphytic herbs without pseudobulbs, the linear, undivided, pseudomonopodial, foliaceous stems erect or pendulous, entirely enveloped in the short, equitant, distichously imbricating, coriaceous leaves. Inflorescences short 1- or 2-flowered scapes or sometimes abbreviated few-flowered panicles, produced from the upper leaf axils. Flowers of moderate size to small, usually yellow, on elongate, filiform pedicels, often subtended by conspicuous membranaceous bracts. Sepals

subequal, free, spreading or with the laterals reflexed. Petals subequal to the sepals or broader. Lip usually complexly 3-lobed, rarely entire, usually conspicuously exceeding the sepals in length, the lateral lobes (if present) often linear, rather long, divaricate or antrorsely incurving, the mid-lobe variously 2- to 4-lobulate, the disk with a papillose, denticulate or tuberculate callus. Column very short, with two broad wings or auricles, the base without a foot. Anther terminal, operculate, incumbent, imperfectly 2-celled; pollinia 2, waxy.

A rather perplexing genus of perhaps 30 species of American epiphytes, ranging from Mexico to Peru and Brazil. Six species, and one variety, are known to occur in Panama.

a. Inflorescences relatively large, spreading, divaricate panicles..... 1. L. ACUTA
aa. Inflorescences very short, compact, subsessile panicles or 1- to 2-flowered scapes.
  b. Lip entire or subentire, without distinct linear lobes at the base. Inflorescences 1-flowered.
    c. Leaves acute. Apex of the lip deeply emarginate..... 7. L. PITTIERI
    cc. Leaves broadly obtuse. Apex of the lip entire..... 5. L. OBTUSATA
  bb. Lip with distinct linear lobes at the base. Inflorescences 1-flowered or shortly racemose or paniculate.
    c. Flowers very small, the lip usually less than 4 mm. long. Leaves obliquely truncate or obtuse at the apex..... 4. L. MICRANTHA
    cc. Flowers relatively large, the lip 7 mm. long or more. Leaves acute or subacute at the apex.
      d. Mid-lobe of the lip subpandurate, conspicuously broader at the apex than at the base, with a distinct isthmus or constriction between the apical portion and the smaller lateral lobules..... 6. L. OERSTEDII
      dd. Mid-lobe of the lip either subquadrate or conspicuously broader at the base than at the apex.
        e. Mid-lobe subquadrate, composed of 4 distinct or obscure, subequal lobules..... 2. L. AMOENA
        ee. Mid-lobe quadrate-triangular, more or less distinctly 3-parted..... 3. L. AMOENA var. TRIANGULABIA

1. LOCKHARTIA ACUTA (Lindl.) Rchb. f. in Bot. Zeit. 10:767. 1852.

Fernandezia acuta Lindl. in Bot. Reg. 21: *t. 1806.* 1836.
Lockhartia pallida Rchb. f. in Bonplandia 2:14. 1854.

Caespitose, epiphytic herbs with flattened, pendulous, foliaceous stems, 15–50 cm. long and 1–2 cm. wide. Leaves, as normally seen in profile, rather obliquely triangular, acute or sharply apiculate at the apex, coriaceous, 12–30 mm. long and 4–10 mm. wide. Inflorescences usually 1 to 3 relatively large, spreading, divaricate, few- to many-flowered panicles up to about 8 cm. long, produced from the subterminal leaf axils. Flowers small, white with a yellow lip, less than 10 mm. in diameter when spread out, on slender filiform pedicels subtended by small, subcordate, papery bracts. Sepals free, subequal, spreading, ovate, obtuse, concave, 3–4 mm. long and about 2 mm. wide. Petals elliptic-oblong, obtuse, 4–5 mm. long and about 2 mm. wide. Lip more or less rectangular in outline, about 6 mm. long and 4 mm. wide, the basal half subquadrate, slightly concave, with narrow, erect, lateral margins, the sessile base adnate to the base of the column, the mid-lobe 4-parted, usually somewhat reflexed, the lateral lobules acute, spreading or

Fig. 209. *Lockhartia acuta*

divaricately extrorse, the projecting central lobule oblong to subquadrate, the apex deeply emarginate, the disk with a bifid, puberulent callus, the concave base under the column with a minute, semiglobose, densely papillose, shortly stipitate process. Column very short, 1–1.5 mm. long, with broadly spreading triangular or auriculate wings on each side of the stigma, the base without a foot.

Panama, Colombia, Venezuela, and Trinidad.

CANAL ZONE: Pedro Miguel, sea level, *Powell 3051;* upper Chagres River, Madden Lake region, 70–75 m., *Steyermark 17515.* PANAMÁ: hills near Panama City, sea level, *Powell 52;* forests of Juan Díaz, near Panama City, 20–50 m., *Pittier 2551;* Chiva-Chiva, sea level, *Powell 3014, 3019;* San José Island, Perlas Archipelago, *Johnston 1217.* COLÓN: Río Gatuncillo, vicinity Santa Rosa, 25 m., *Allen 4253.*

A common lowland species with very small flowers, readily recognizable by the relatively long, pendulous, foliaceous stems and the conspicuous, broadly paniculate inflorescences.

2. LOCKHARTIA AMOENA Endres & Rchb. f. in Gard. Chron. 666. 1872.

Lockhartia costaricensis Schltr. in Fedde Rep. Sp. Nov. 3:81. 1906.
Lockhartia-grandibracteata Kränzl. in Engler, Pflanzenr. IV, Fam. 50 (Heft 83):15. 1923.

Caespitose, epiphytic herbs with erect or pendulous, flattened, foliaceous stems 12–40 cm. long and 1.4–2.5 cm. wide. Leaves narrowly triangular in profile, subacute, coriaceous, 1.5–3.5 cm. long and 0.4–1.0 cm. wide. Inflorescences short, compact, few-flowered panicles, up to about 3 cm. long. Flowers relatively large for the genus, on long filiform pedicels subtended by conspicuous, ovate-cordate, membranaceous bracts. Sepals free, subequal, slightly concave, yellow, the dorsal sepal erect or somewhat reflexed, ovate, obtuse, with a minute, terminal apicule, 5–6 mm. long and about 4 mm. wide, the lateral sepals strongly reflexed in natural position, elliptic-lanceolate, subacute, 5–6 mm. long and about 4 mm. wide. Petals somewhat longer than the sepals, yellow, elliptic-oblong, obtuse, incurving, the lateral margins conduplicately reflexed in natural position, 5–7 mm. long and about 4 mm. wide when spread out. Lip complexly 3-lobed, yellow, with reddish brown markings at the base, about 10 mm. long and 8 mm. wide, the lateral lobes linear-ligular, acute, antrorsely incurving in natural position, the mid-lobe subquadrate, distinctly or obscurely 4-lobulate, with undulate margins, the truncate apex with a deep central sinus, the basal lobules equaling or somewhat exceeding the 2-parted mid-lobule in width when spread out, very strongly reflexed in natural position, the disk with a linear, truncate, papillose callus. Column very short, with broadly spreading, lateral wings.

Costa Rica and Panama.

COCLÉ: hills north of El Valle de Antón, 1000 m., *Allen 2313;* mountains beyond La Pintada, 400–600 m., *Hunter & Allen 586.* CHIRIQUÍ: Palo Alto Hill, 4000–5000 ft., *Powell 362;* vicinity Casita Alta, Finca Lérida, eastern slopes of Chiriquí Volcano, 1500–2000 m., *Woodson, Allen & Seibert 966.*

A variable and rather perplexing highland species with relatively large, attractive flowers. It is probably allied to *L. Oerstedii,* but differs in the mid-lobe of the lip, which is more or less subquadrate and 4-lobulate, the basal half equaling or exceeding the apical half in width.

3. LOCKHARTIA AMOENA Endres & Rchb. f. var. TRIANGULABIA C. Schweinf. & P. H. Allen in Bot. Mus. Leafl. Harv. Univ. 13:150. 1948.

Lockhartia triangulabia A. & S. in Sched. Orch. 8:80. 1925.

Vegetative parts and inflorescences apparently as in the type. Sepals subequal, free, probably more or less reflexed in natural position, about 5.4 mm. long and 3 mm. wide, the dorsal sepal ovate, subacute, the lateral sepals rather obliquely elliptic-oblong, obtuse, all three sepals dorsally mucronate at the apex. Petals oblong, obtuse, about 5.4 mm. long and 3 mm. wide. Lip broadly quadrate-triangular in outline, complexly 5-lobulate, about 7.2 mm. long and 10 mm. wide at the base, the lateral lobes rather obliquely ligular, obtuse, the mid-lobe more or less 3-parted, the basal lobules triangular, the basal half of the mid-lobe about twice as wide as the subquadrate, emarginate apical half, the disk with a linear-oblong, minutely papillose callus, the base under the column thickened into a semiorbicular minutely papillose boss.

Panama.

CHIRIQUÍ: without definite locality, 4000–5000 ft., *Powell 362-A.*

Lockhartia amoena, as represented by the quite numerous specimens available for study, exhibits a distinct tendency to vary from a condition in which the basal and apical halves of the 4-parted mid-lobe are of subequal width, to one in which the bifid, apical segment is considerably narrower. Our present single specimen apparently represents an extreme example of this tendency and seems sufficiently distinctive to warrant varietal rank.

4. LOCKHARTIA MICRANTHA Rchb. f. in Bot. Zeit. 10:768. 1852.

Lockhartia chiriquiensis Schltr. in Fedde Rep. Sp. Nov. 12:215. 1913.
Lockhartia Lankesteri Ames, in Sched. Orch. 5:36. 1923.

Caespitose, epiphytic herbs with erect or pendulous, flattened, foliaceous stems typical of the genus, 5–40 cm. long and 1–2 cm. wide. Leaves equitant, coriaceous, in profile narrowly triangular with obliquely truncate or obtuse apices, 0.8–2 cm. long and 0.35–1.0 cm. wide. Inflorescences simple 1- to 3-flowered scapes or abbreviated, few-flowered panicles up to about 2 cm. long, produced from the central or subterminal leaf axils. Flowers small, yellow, on slender, filiform pedicels subtended by ovate-cordate, membranaceous bracts. Sepals subequal, free, spreading, concave, ovate to elliptic-oblong, acute and apiculate, 2.5–4 mm. long and 2–3 mm. wide. Petals broadly ovate to elliptic-ovate, obtuse, 2.5–4 mm. long and 1.5–2 mm. wide. Lip complexly 3-lobed, 2.5–5 mm. long and 2.5–5 mm. wide, the lateral lobes linear-ligular, obtuse, spreading or reflexed, the mid-lobe

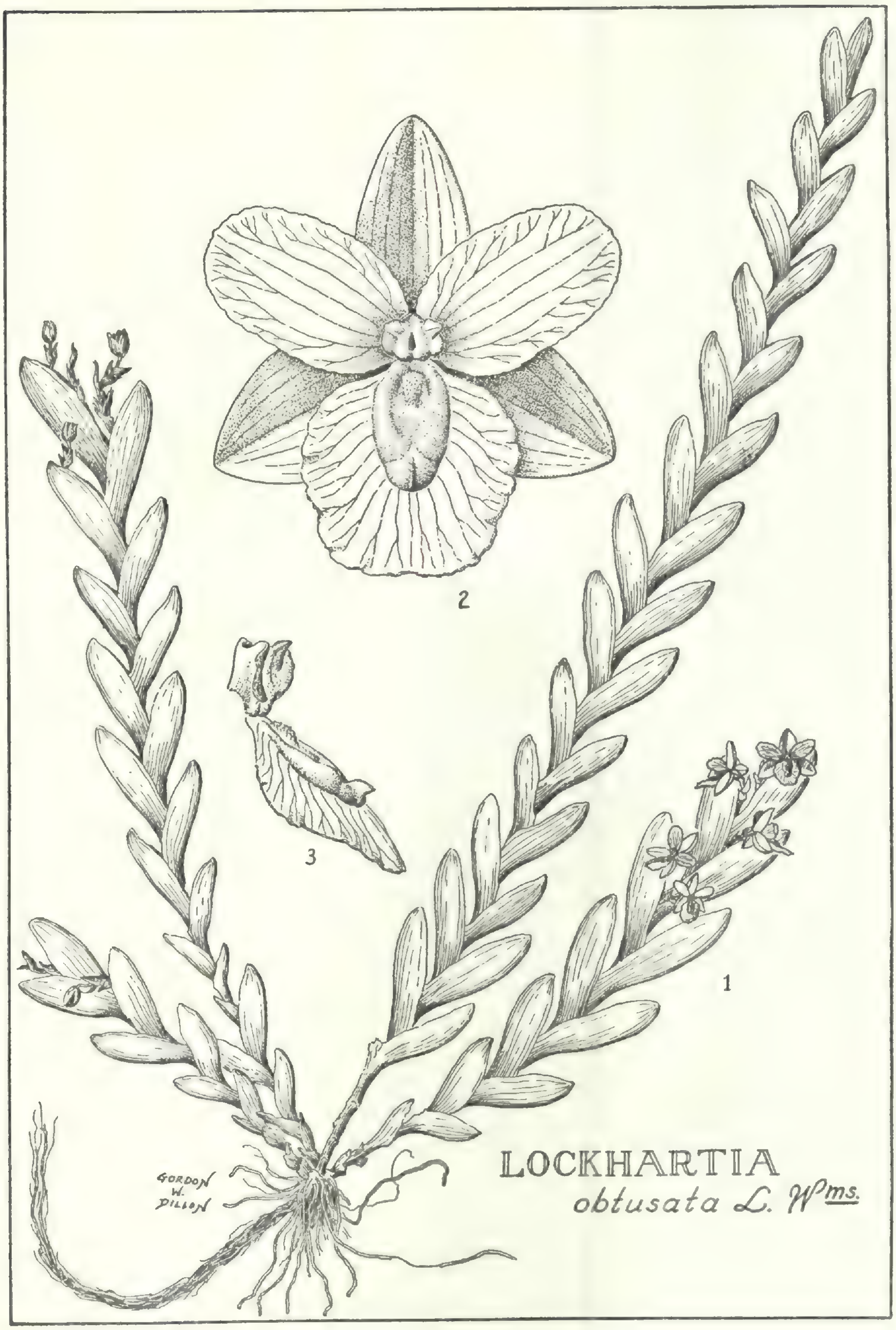


Fig. 210. *Lockhartia obtusata*

rhombic-obovate to obovate, the lateral margins obscurely lobulate, the apex deeply retuse, the disk with a low, slightly concave, more or less bifid callus. Column very short, with spreading lateral wings, the base without a foot.

Nicaragua to Surinam (fide Kränzlin).

CANAL ZONE: Balboa, on mango tree, *Standley 25494;* Río Pedro Miguel, near East Paraiso, *Standley 29984;* Las Cruces, *Powell 3189;* Miraflores, *Powell 3203;* Pedro Miguel, *Powell 3049;* drowned forests of the Quebrada Tranquilla, Madden Lake region, *Dodge & Allen 17325;* Río Indio, Madden Lake region, *Steyermark & Allen 17437, 17440.* PANAMÁ: Río La Maestra, coastal area east of the Río Bayano, 0–25 m., *Allen 61.* COCLÉ: hills north of El Valle de Antón, 1000–1200 m., *Allen 2318, 2903, 3420, 3939, 4259.* VERAGUAS: vicinity Santa Fé, 1000 ft., *Allen 4429;* vicinity Bahía Honda, *Taylor 1510.* CHIRIQUÍ: vicinity San Felíx, 0–120 m., *Pittier 5286;* without definite locality, 4000 ft., *Powell 3476.*

A common small-flowered species somewhat reminiscent of *Lockhartia acuta,* but distinguished by the usually shorter foliaceous stems, much shorter inflorescences, yellow flowers, and differently shaped lip.

5. LOCKHARTIA OBTUSATA L. Wms. in Amer. Orch. Soc. Bull. 9:209, *t. 8.* 1941.

Caespitose, epiphytic herbs with broad, strongly flattened, foliaceous stems up to about 35 cm. tall and 2.5–3.5 cm. wide. Leaves equitant, distichously imbricating, coriaceous, obliquely oblong as seen in profile, obtuse, 2–4 cm. long and 0.5–1.0 cm. wide. Inflorescences short, condensed racemes from the upper leaf axils. Flowers relatively large and attractive, bright yellow with a conspicuous orange callus at the base, apparently produced singly in succession from the terminal cluster of ovate, acute, papery bracts. Sepals subequal, free, spreading, ovate, obtuse to shortly acute, minutely apiculate, about 9 mm. long and 6 mm. wide. Petals elliptic-oblong, obtuse, 9–10 mm. long and 5–6 mm. wide. Lip entire, suborbicular, slightly convex, 9–10 mm. long and 9–10 mm. wide, the anterior margin sometimes slightly retuse, the disk with an elliptic-oblong to obovate, obtuse callus, about 5 mm. long and 3–4 mm. wide, the apex conspicuously thickened and papillose, with a short, erect, acute, central spur. Column about 2 mm. long, with conspicuous lateral wings, the base without a foot.

Panama.

COCLÉ: hills north of El Valle de Antón, 1000 m., *Allen 2160, 3550.*

A strikingly handsome highland species apparently allied to *L. Pittieri,* but distinguished by the broad, obtuse leaves, the larger flowers, and the unique, entire, suborbicular lip.

6. LOCKHARTIA OERSTEDII Rchb. f. Xenia Orch. 1:100, 105, *t. 40.* 1855.

Lockhartia verrucosa Rchb. f. in Hamb. Gartenzeit. 15:53. 1859.
Lockhartia lamellosa Rchb. f. loc. cit. 16:300. 1860.
Fernandezia robusta Batem. in Bot. Mag. *t. 5592.* 1866.
Lockhartia robusta (Batem.) Schltr. in Fedde Rep. Sp. Nov. 3:82. 1906.

Caespitose, epiphytic herbs with strongly flattened, foliaceous stems 7–40 cm. long and 0.8–1.5 cm. wide. Leaves narrowly triangular as seen in profile, acute, 1–3 cm. long and 0.4–0.8 cm. wide. Inflorescences very short, 1- to 3-flowered racemes produced from the axils of the upper leaves. Flowers very variable in size, but often relatively large and attractive, the pedicels subtended by papery, ovate-cordate bracts. Sepals usually strongly reflexed, sometimes slightly concave, yellow, the laterals sometimes spotted with red, elliptic-oblong to ovate, obtuse to shortly acute, 4–8 mm. long and 3–5 mm. wide. Petals yellow, sometimes spotted red, oblong-ovate to broadly and obliquely ligular, obtuse or slightly retuse at the apex, antrorsely incurving in natural position, the lateral margins usually more or less undulate and strongly reflexed, 4–8 mm. long and 3–6 mm. wide. Lip complexly 3-lobed, 7–12 mm. long and 6–14 mm. wide, yellow with red or reddish brown markings at the base, the lateral lobes linear-ligular, obtuse or obliquely acute, spreading or antrorsely incurving in natural position, the mid-lobe more or less pandurate, 4-lobulate, the basal half distinctly narrower than the apical half, the small basal lobules rounded or obliquely triangular, strongly reflexed in natural position, sometimes confluent with the bases of the linear lateral lobes, the center of the mid-lobe with a distinct constriction which is often prolonged into a short isthmus, the apical lobule usually abruptly dilated, 2-parted with a deep central sinus, the disk with a narrowly flabellate or sometimes linear, strongly verrucose callus, extending to the median constriction. Column with spreading, minutely denticulate or crenulate lateral wings.

Mexico, Guatemala, Honduras, Costa Rica, and Panama.

CHIRIQUÍ: Llano del Volcán, southwestern slopes of Chiriquí Volcano, 1500 m., *Allen & Fairchild 3502;* vicinity Cerro Punta, headwaters of the Río Chiriquí Viejo, 2000 m., *Allen & Fairchild 3493;* valley of the upper Río Chiriquí Viejo, vicinity Monte Lirio, 1300–1900 m., *Seibert 132, 133, 186;* without definite locality, 4000–4500 ft., *Powell 3344, 3352;* vicinity Bajo Mono, headwaters of the Río Caldera, 4500 ft., *Davidson 584;* vicinity Finca Lérida, eastern slopes of Chiriquí Volcano, 1750 m., *Woodson & Schery 236;* forested slopes along Quebrada Velo, 5000 ft., *Allen 4743;* bamboo-oak forest, south of Finca Lérida, eastern slopes of Chiriquí Volcano, 6000–7000 ft., *Allen 4764;* forested hills east of Boquete, 4500–6500 ft., *Allen 4666.*

A common, attractive highland species apparently closely allied to the South American *L. lunifera* (Lindl.) Rchb. f. In Panama, the species is readily separable from its nearest ally, *L. amoena,* by the subpandurate mid-lobe of the lip, which is always broadest at the apex.

7. LOCKHARTIA PITTIERI Schltr. in Fedde Rep. Sp. Nov. 12:216. 1913.

Lockhartia variabilis A. & S. in Sched. Orch. 8:81. 1925.

Caespitose, epiphytic herbs with distichous, foliaceous stems up to about 20 cm. tall and 2.5–4.5 cm. wide. Leaves linear-lanceolate to narrowly triangular as seen in profile, obliquely acute to acuminate, 2–3.5 cm. long and 0.4–0.9 cm. wide. Inflorescences very short, apparently solitary, 1-flowered scapes produced from the axils of the upper leaves. Flowers of moderate size for the genus, yellow

with an orange callus at the base. Sepals elliptic-lanceolate, acute, with apiculate tips, 3.9–4.9 mm. long and about 2 mm. wide. Petals somewhat broader than the sepals, elliptic-oblong to suborbicular, obtuse to acute, 4–5 mm. long and 2.4–3.2 mm. wide. Lip oblong-quadrate, 7–8 mm. long and 5–6.4 mm. wide, slightly convex, the apex deeply emarginate, the lateral margins sometimes obscurely lobular, the disk with an elliptic-oblong to ovate-oblong callus, the margins elevated, the apex conspicuously thickened and minutely papillose, with an erect, subacute, central spur, the inner elliptic depression with a low, rounded boss.

British Honduras, Costa Rica, and Panama.

CANAL ZONE: vicinity Bohío, *Pittier 3401;* Fort Sherman and mouth of the Chagres River, *Powell 372;* wooded hills near Frijoles, sea level, *Powell 355;* Cativo-Porto Bello trail, *Powell 361.* DARIÉN: vicinity Marragantí, 10–200 ft., *R. S. Williams 1008.*

DOUBTFUL SPECIES

LOCKHARTIA MIRABILIS Rchb. f. Xenia Orch. 1:100, 106, *t. 40, figs. 11–12.* 1855.

Apparently described from flowering material only, without vegetative parts. The figures in the 'Xenia Orchidaceae' might be poor drawings of what we know as *Lockhartia Oerstedii,* seen in natural position, with the lateral lobules of the mid-lobe reflexed. Since both of these concepts seem very close to that of the South American *L. lunifera* Rchb. f., and since *L. mirabilis* is absent from all recent collections in Panama, it would seem best to exclude it, pending the rather remote possibility of direct examination of type material of both this and *L. lunifera.*

LOCKHARTIA ELEGANS Hook. in Bot. Mag. *t. 2715.* 1827.

A South American species, apparently having the northern limit of its range in Trinidad. Listed by Schlechter from Panama, but absent from all collections.

LOCKHARTIA OBTUSIFOLIA Regel in Ann. Sci. Nat. VI, 2:378. 1856.

A Colombian species, doubtfully listed by Kränzlin from Panama. Absent from all collections.

82. ORNITHOCEPHALUS Hook.

ORNITHOCEPHALUS Hook. Exot. Fl. 2: *t. 127.* 1825; Benth. & Hook. Gen. Pl. 3:568. 1883.

Small, epiphytic herbs without pseudobulbs, the equitant, fleshy or coriaceous leaves distichously imbricating and forming a broad or narrow fan, the blades articulated below, those at the base of the fan caducous, the persistent sheathing bases sometimes thickened and resembling pseudobulbs. Inflorescences 1 to several slender, erect or pendulous racemes produced from the leaf axils. Sepals subequal, free, spreading, often concave. Petals subequal to the sepals or larger and flabellate. Lip entire or 3-lobed, the subsessile base continuous with the base of the column, the lateral lobes (if present) membranaceous or sometimes thickened, the mid-lobe short or more frequently elongate, often inflexed, the disk with a fleshy, bifid, bialate or bicornute callus. Column short, rather stout, without wings or ap-

pendages, the rostellar process very long and attenuate, the base of the column without a foot. Anther terminal, operculate, incumbent, imperfectly 2-celled, produced above the cells into an attenuate appendage resting on the rostellar process, sometimes exceeding it in length, the column and anther resembling the head and beak of a bird (genus unknown!); pollinia 4, waxy.

A small genus of dwarf, pseudobulbless, epiphytic herbs, ranging from Mexico to Brazil. Four species are known from Panama.

a. Rachis of the inflorescence densely glandular-hispid.
  b. Lip linear-navicular, incurving, the fleshy basal plate with 2 divergent horns..... 1. O. BICORNIS
  bb. Lip subquadrate-cochleate, without 2 divergent horns at the base..... 2. O. COCHLEARIFORMIS
aa. Rachis of the inflorescence glabrous or minutely puberulent.
  b. Flowers relatively large. Lip panduriform, broadest at the base, with a distinct fleshy, 2-parted callus..... 4. O. POWELLII
  bb. Flowers small. Lip linear-navicular, incurving, the lateral lobes thickened and erect..... 3. O. INFLEXUS

1. ORNITHOCEPHALUS BICORNIS Lindl. in Bot. Voy. Sulphur, 172. 1843.

Ornithocephalus xiphochilus Schltr. in Fedde Rep. Sp. Nov. 3:251. 1906.
Zygostates costaricensis Nash, in Bull. Torr. Bot. Club 34:122, *t. 8*. 1907.
Ornithocephalus lanuginosus Ames, in Proc. Biol. Soc. Wash. 34:152. 1921.
Ornithocephalus diceras Schltr. in Fedde Rep. Sp. Nov. Beih. 17:87. 1922.

Small, epiphytic herbs 3.5–12 cm. tall, the equitant leaves distichously arranged in the form of a broad fan. Leaf blades articulated to the conduplicate, imbricating, persistent bases, coriaceous, lanceolate to gladiate as seen in profile, obliquely acute, 2–9 cm. long and 0.4–1.2 cm. wide. Inflorescences 1–10 slender, many-flowered, axillary racemes about equaling the leaves in length, the rachis densely hispid with spreading glandular hairs. Flowers small, greenish or yellowish, on short hispid pedicels subtended by ovate, acute, membranaceous, ciliate bracts. Sepals suborbicular, concave, about 2 mm. in diameter, the reverse surfaces somewhat hispid, with a central elevated keel, terminating in a short mucro. Petals subequal to the sepals, very shortly clawed at the base, the blades orbicular, concave, about 2 mm. in diameter, the reverse surfaces more or less hispid, with a ciliate central keel, terminating in a short mucro. Lip entire, linear-navicular, acute, strongly incurving, about 4–5 mm. long when spread out, the base with a fleshy, papillose, subquadrate to suborbicular, cushion-like callus, produced at the sides into 2 short, divergent, horn-like appendages each about 1 mm. in length.

Guatemala, Honduras, Costa Rica, and Panama.

CANAL ZONE: drowned forest of the Quebrada Ancha, upper Madden Lake region, 70 m., *Steyermark & Allen s. n.;* vicinity Salamanca Hydrographic Station, Gorge of the Río Pequení, Madden Lake area, 70–80 m., *Dodge, Steyermark & Allen 16969.* PANAMÁ: hills east of Panama City, sea level, *Powell 174;* edge of forest along Panama-Pacora road, near Río Tecúmen, *Killip 3314;* without definite locality, *Sinclair s. n.* VERAGUAS: without definite locality, *Hinds s. n.*

Fig. 211. *Ornithocephalus bicornis*

A common, small-flowered lowland species distinguished from *O. cochleariformis* by the elongate, narrowly navicular, incurving lip and from *O. inflexus* by the densely hispid rachis and the divergent horns of the basal callus.

2. Ornithocephalus cochleariformis C. Schweinf. in Bot. Mus. Leafl. Harv. Univ. 4:124. 1937.

Epiphytic herbs 3.5–12 cm. tall. Leaves as seen in profile narrowly elliptic-oblong to broadly ensiform, acute or obliquely acute, 3–7.5 cm. long and 0.7–1.5 cm. wide, the blades articulated to the oblong, persistent, conduplicate bases. Inflorescences 1–8 slender, arching or pendulous racemes up to about 9 cm. long, the rachis densely glandular-hirsute. Flowers of moderate size for the genus, on slender hirsute pedicels subtended by broadly ovate to suborbicular bracts with glandular-ciliate keels and margins. Sepals suborbicular to obovate, concave,

white, about 3 mm. in diameter, the reverse surfaces and margins densely glandular-hirsute, the lateral sepals slightly oblique, with lacerate keels on the outer surfaces. Petals subequal to sepals, white, broadly obovate, concave, the outer surfaces ciliate, with a conspicuously lacerate central keel. Lip deep green, entire, broadly calceiform, deeply concave, about 4.2 mm. long and 3.2 mm. wide, the truncate or subcordate base adnate to the base of the column, the shortly acute apex strongly inflexed, the disk transversely thickened, minutely papillose, the lateral margins decurrent, with 2 short, lateral, acute swellings, finally truncately converging below at the base of the inner concavity of the lip.

Panama.

COCLÉ: lower valley and marshes along the Río Antón, 600 m., *Hunter & Allen 383, Allen 3920, 4233;* rim of El Valle de Antón, 2500 ft., *Purdom s.n.;* hills north of El Valle de Antón, 1000 m., *Allen 2292.*

A common highland species of the region of El Valle de Antón, in Coclé Province. It is distinguished by the densely glandular-hirsute outer surfaces of the sepals and petals, and by the broadly calceiform lip.

3. ORNITHOCEPHALUS INFLEXUS Lindl. in Ann. Nat. Hist. I, 4:384. 1840.

Ornithocephalus mexicanus A. Rich. & Gal. in Ann. Sci. Nat. III, 3:24. 1845.
Ornithocephalus elephas Rchb. f. in Walp. Ann. 6:493. 1863.
Ornithocephalus Pottsiae S. Wats. in T. Brigh. Guatem. Append. 429. 1887.
Ornithocephalus Tonduzii Schltr. in Beih. Bot. Centralbl. 36^2:420. 1918.

Dwarf, epiphytic herbs, the equitant, imbricating leaves forming a fan as in the genus. Leaves linear-lanceolate to ensiform as seen in profile, acute to acuminate, coriaceous, 4.5–8 cm. long and 0.25–0.5 cm. wide, the blades articulated to the persistent, conduplicate bases. Inflorescences 1 to several slender racemes up to about 8 cm. long, produced from the axils of the leaves, the rachis glabrous or minutely puberulent. Flowers small, on slender pedicels subtended by oblong-lanceolate, acute, minutely ciliate bracts. Sepals suborbicular, concave, about 2 mm. in diameter, the reverse surfaces essentially glabrous, with distinct central keels, terminating in a short mucro. Petals broadly flabellate-cuneate to dolabriform, about 2 mm. long and 3 mm. wide. Lip entire, linear-ligular, acute to acuminate, navicular, usually inflexed, about 5 mm. long and 2 mm. wide, the base thickened into a short bialate or biauriculate callus, the fleshy rounded or subquadrate wings usually erect or with the upper margins converging.

Mexico, British Honduras, Guatemala, Honduras, Costa Rica, and Panama.

CHIRIQUÍ: without definite locality, 4000 ft., *Powell 431.*

4. ORNITHOCEPHALUS POWELLII Schltr. in Fedde Rep. Sp. Nov. Beih. 17:88. 1922.

Epiphytic herbs 5–8 cm. tall, the equitant leaves distichously arranged in the form of a broad fan, as in the genus. Leaves subfalcately ligular as seen in profile, obliquely acute, often shortly apiculate, coriaceous, 3.5–6.5 cm. long and 0.6–1.2

cm. wide, the blades articulated with the very short, conduplicate, persistent bases. Inflorescences 1 or 2 slender racemes up to about 9 cm. long, produced from the leaf axils, the rachis laterally compressed, narrowly winged, subglabrous to puberulent. Flowers rather large for the genus, deep green with a white basal callus, the short, angulate pedicels subtended by elliptic-ovate, acute bracts which have a strongly developed keel and minutely ciliate margins, the apices of the bracts shortly mucronate. Sepals spreading or reflexed, ovate to oblong-ovate, concave, about 4 mm. long and 2.5–3 mm. wide, the outer surfaces with a distinct central keel, terminating in a short mucro, the margins of the sepals ciliate or serrulate. Petals much broader than the sepals, obovate-cuneate to obovate-flabellate, about 6 mm. long and 8 mm. wide, the upper rounded margins minutely ciliate to serrulate. Lip panduriform, obscurely 3-lobed, about 1 cm. long and 0.5 cm. wide at the base, the broadly ovate to subcordate basal half adnate to the base of the column, the anterior margins converging in an elongate isthmus, the subflabellate apex rather abruptly dilated and truncate, with serrulate margins, the apical half of the lip usually porrect in natural position, the disk with a prominent fleshy, porrect, divergently 2-lobulate callus.

Panama.

PANAMÁ: foothills east of Panama City, sea level, *Powell 231;* San Juan de Pequení [now under water in the Madden Lake area], *Powell 3279.*

The largest-flowered species of the genus in our area. The pair of low, divergent, linear calli described by Schlechter is an optical illusion produced in translucent liquid material by the shadows of the margins of the lateral sepals which rest against the back of the lip.

82-A. OAKES-AMESIA C. Schweinf. & P. H. Allen

OAKES-AMESIA C. Schweinf. & P. H. Allen in Bot. Mus. Leafl. Harv. Univ. 13:133, *t. 10.* 1948.

Dwarf, epiphytic herbs without pseudobulbs, the equitant, coriaceous leaves distichously imbricating and forming a broadly radiate cluster. Leaf blades ensiform as seen in profile, obliquely acute, articulated to the conduplicate bases. Inflorescences erect or arching racemes produced from the subterminal leaf axils. Flowers small, the short pedicels subtended by elliptic-ovate, acuminate bracts. Sepals free, subequal, spreading, or the laterals reflexed, elliptic-oblong, subacute, the reverse surfaces with a distinct central keel. Petals much larger than the sepals, spreading, broadly obovate-flabellate. Lip somewhat fleshy, sharply 3-lobed, exceeding the lateral sepals in length, the base sessile and continuous with the base of the column, the lateral lobes very prominently developed, erect in natural position, the mid-lobe more or less subquadrate when seen from above, somewhat dilated and obscurely biauriculate at the abruptly truncate apex, the small lateral auricles obliquely acute, the under-surface of the mid-lobe produced into a very prominent, obliquely triangular, obtuse to subacute, laterally compressed keel

which is apparently hollow with a narrow transverse opening at the apex of the lip, the disk with a low, linear-ligular, truncate, densely papillose callus. Column very slender and subterete below, somewhat dilated above, wingless and footless, a little below the lightly arcuate apex with a very large, distinctly 3-lobulate rostellar process. Anther suborbicular, terminal, operculate, incumbent, imperfectly 2-celled; pollinia 4, apparently cartilaginous.

A genus of dwarf highland epiphytes thus far known only from Panama. The plants strongly resemble those of the allied genus *Ornithocephalus*, but the flowers are amply separated by the very large, 3-lobulate rostellar process, the relatively very short terminal appendage of the anther, the short, abruptly truncate, sharply 3-lobed lip, the prominent, apparently hollow keel of the lip, the linear-ligular callus, and other characters.

1. OAKES-AMESIA CRYPTANTHA C. Schweinf. & P. H. Allen in Bot. Mus. Leafl. Harv. Univ. 13:134, *t. 10.* 1948.

Dwarf, epiphytic herbs, the leaves forming a broadly radiate cluster 4 cm. tall and 7.5 cm. wide. Leaf blades ensiform as seen in profile, obliquely acute, 1.8–3.9 cm. long and 0.3–0.5 cm. wide, articulated to the conduplicate bases, the plants identical in vegetative appearance with those of *Ornithocephalus inflexus*. Inflorescences 1 to 3 erect or arching racemes about 5.5 cm. long, produced from the subterminal leaf axils, the rachis slightly fractiflex and rather complanate, narrowly triangular in cross-section. Flowers small, the sepals and petals white, the lip dark green marked with white, the short pedicels subtended by long, elliptic-ovate, acuminate bracts which have strongly developed keels on the lower surfaces, the bracts conspicuously exceeding the floral pedicels in length. Sepals free, subequal, elliptic-oblong, subacute, slightly concave, unevenly serrulate, irregularly glandular-verrucose on both surfaces, the reverse surfaces with a distinct central keel, terminating in an elongate spinous process, the dorsal sepal spreading or slightly reflexed, about 2.7 mm. long and 1.25 mm. wide, the lateral sepals strongly reflexed, about 2.9 mm. long and 1.5 mm. wide. Petals much larger than the sepals, spreading, broadly obovate-flabellate, the abruptly truncate blades with shallow transverse concavities below the irregularly serrulate upper margins, the blades about 3 mm. long and 3 mm. wide at the apex, both the frontal and reverse surfaces irregularly glandular-verrucose. Lip rather fleshy, sharply 3-lobed, the sessile base continuous with the base of the column, the very prominent lateral lobes rather obliquely oblong, truncate, erect in natural position and somewhat antrorse, about 1.5 mm. long and 1 mm. wide, minutely ciliate, the mid-lobe subquadrate when seen from above, somewhat dilated and obscurely biauriculate at the abruptly truncate apex, the small lateral auricles obliquely acute, the undersurface of the mid-lobe produced into a very prominent, obliquely triangular, obtuse to subacute, laterally compressed keel which is apparently hollow with a narrow, transverse opening at the apex of the lip, the entire lip sparsely and irregularly glandular-verrucose, about 4 mm. long and 2.5 mm. wide at the apex,

the disk with a low, linear-ligular, abruptly truncate, densely papillose callus. Column very slender below, wingless, footless, below the slightly arcuate apex extends a very large, 3-lobulate rostellar process which considerably exceeds the rest of the column in length and bulk, 3 mm. long and 1 mm. wide, the lateral lobules semiorbicular, abruptly deflexed in natural position, the porrect, slightly undulate apical lobule more or less terete, all 3 lobules of the rostellar process rather densely glandular-verrucose. Column above the rostellar process short, slightly arcuate, the anther suborbicular, terminal, operculate, incumbent, imperfectly 2-celled, with a slender, ligular, acuminate appendage, the rostellar process and anther rather resembling the head and folded legs of a praying mantis when seen in profile.

Panama.

COCLÉ: Cerro Pajita, hills north of El Valle de Antón, 1000–1200 m., *Allen & Allen 4196*.

83. NOTYLIA Lindl.

NOTYLIA Lindl. in Bot. Reg. 11: sub *t. 930*. 1825; Rchb. f. Xenia Orch. 1:49. 1854; Benth. & Hook. Gen. Pl. 3:586. 1883.

Tridachne Liebm. ex Lindl. in Paxt. Flow. Gard. 3:45. 1852-53, nom nud.
Macroclinium Barb. Rodr. Gen. & Spec. Orch. Nov. 2:236. 1882.

Small, epiphytic herbs with or without pseudobulbs. Leaves usually flat, rarely equitant, coriaceous or fleshy. Inflorescences arching or pendulous, few- to many-flowered racemes, or rarely panicles, produced from the bases of the pseudobulbs or axils of the leaves. Flowers usually small, rarely of moderate size, on slender pedicels, the subtending bracts usually narrow. Sepals subequal, usually narrow, erect or spreading, free or with the laterals more or less connate. Petals subequal to the sepals or smaller. Lip entire or obscurely lobed, usually clawed at the base, rarely sessile, continuous with the base of the column, the lamina triangular or hastate, acuminate, the disk smooth or with a carinate callus. Column erect, terete or sulcate, glabrous, papillose or velutinous, without wings or appendages, the apex usually slightly recurved, the rostellum more or less elongate, acuminate, erect, the base of the column without a foot. Anther erect, oblong, imperfectly 2-celled, above the cells more or less long-appendaged and applied to the rostellum; pollinia 2, waxy.

Small tropical American herbs ranging from Mexico to Brazil. They have been divided by Cogniaux into two well-marked subgenera, in the first of which, EUNOTYLIA, the plants have small but distinct, monophyllous pseudobulbs, with flat leaves; while in the second, MACROCLINIUM, the leaves are equitant and distichously imbricating, the conduplicate bases sometimes enveloping a small complanate pseudobulb. Five species, representing both subgenera, are known from Panama.

a. Leaves equitant, ensiform. Lip cordate-hastate, distinctly 3-lobed. (Subgenus MACROCLINIUM) ..... 2. N. CORDESII
aa. Leaves flat, ligular to oblong-lanceolate. Lip trulliform. (Subgenus EUNOTYLIA).
b. Column distinctly papillose ..... 5. N. PENTACHNE
bb. Column glabrous.
c. Lip about 5 mm. wide at the base ..... 3. N. LATILABIA
cc. Lip less than 3 mm. wide at the base.
d. Dorsal sepal broadly elliptic-oblanceolate, obtuse, about 5 mm. wide, distinctly broader than the lip ..... 4. N. PANAMENSIS
dd. Dorsal sepal linear-lanceolate, subacute, 2 mm. wide or less, distinctly narrower than the lip ..... 1. N. BARKERI

1. NOTYLIA BARKERI Lindl. in Bot. Reg. n. s. 1: Misc. 90. 1838.

Notylia multiflora Hook. in Lond. Jour. Bot. 3:315, *t. 10.* 1844, non Lindl.
Notylia Huegelii Fenzl. in Denkschr. Akad. Wien, Math. Nat. Kl. 2:255. 1850.
Notylia trisepala Lindl. & Paxt., in Paxton's Flow. Gard. 3:45. 1852-53; Bot. Mag. *t. 8306.* 1910.
Tridachne virens Liebm. ex Lindl. & Paxt. loc. cit. 1852-53.
Notylia Tridachne Lindl. & Paxt. loc. cit. 1852-53.
Notylia bipartita Rchb. f. Xenia Orch. 1:47. 1854.
Notylia tamaulipensis Rchb. f. in Hamb. Gartenzeit. 16:281. 1860.
Notylia guatemalensis S. Wats. in Proc. Amer. Acad. 22:477. 1887, non Schltr.
Notylia angustilancea Schltr. in Orchis 8:135, *t. 4, figs. 8–13.* 1914.
Notylia guatemalensis Schltr. in Fedde Rep. Sp. Nov. 15:208. 1918, non S. Wats.
Notylia Bernoullii Schltr. in Beih. Bot. Centralbl. 36^2:502. 1918, nomen.
Notylia Pittieri Schltr. loc. cit. 418. 1918.
Notylia turialbae Schltr. in Fedde Rep. Sp. Nov. Beih. 19:145. 1923.
Notylia Brenesii Schltr. loc. cit. 249. 1923.

Small, epiphytic herbs with oblong, compressed, monophyllous pseudobulbs up to about 2.5 cm. long and 1.0 cm. wide, the bases enveloped in several imbricating bracts, the uppermost 1 or 2 of which are conspicuously foliaceous. Leaves and bract blades ligular, obtuse to subacute, coriaceous, up to about 18 cm. long and 0.8–4 cm. wide. Inflorescences 1 or 2 arching or pendulous, densely flowered racemes up to about 30 cm. long but often considerably less, produced from the bases of the pseudobulbs. Flowers small, white, sometimes spotted yellow, on filiform pedicels, subtended by narrow, acuminate bracts. Sepals subequal, more or less spreading, the dorsal sepal free, linear-lanceolate, subacute, concave, somewhat inflexed, 3–6 mm. long and 1–2 mm. wide, the lateral sepals usually more or less connate, rarely free, forming a single bifid segment under the lip, 3–5 mm. long and 1–2 mm. wide, rather obliquely subacute. Petals subfalcately linear-lanceolate, acute, 2.5–5 mm. long and 1–1.5 mm. wide. Lip clawed at the base and continuous with the base of the column, the lamina narrowly triangular, acuminate, 3–5 mm. long and 1–2 mm. wide at the base, the disk usually with a distinct carinate callus. Column slender, erect, terete, 2–3 mm. long, the base without a foot.

Mexico to Panama.

CANAL ZONE: near Balboa, sea level, *Powell 405.* VERAGUAS: Santa Fé, 2500 ft., *Powell 401.* CHIRIQUÍ: without definite locality, 4000 ft., *Powell 427.*

The plants and flowers are quite variable in size and in the degree to which the lateral sepals are connate, but the floral structure otherwise is rather remarkably uniform, particularly in view of the great geographic range. It is difficult to believe that any great weight should be attached to the degree of connation of the lateral sepals since they are found to be very easily separable, both in specimens in liquid and in flowers boiled out for examination, so that one specific concept can be transformed into another simply by a little carelessness with the dissecting instruments!

2. Notylia Cordesii L. Wms. in Ann. Mo. Bot. Gard. 26:286, *t. 21, figs. 3–4.* 1939.

Dwarf, epiphytic herbs with equitant, distichously imbricating leaves, the conduplicate bases enveloping a small, oblong-complanate, monophyllous pseudobulb 1–1.5 cm. long and about 0.5 cm. wide, the plants reminiscent of those of an *Ornithocephalus*. Leaves lanceolate to linear-lanceolate as seen in profile, ensiform, rather obliquely acuminate, the blades articulated to the conduplicate bases, 4–6 cm. long and 0.3–0.5 cm. wide. Inflorescences slender, essentially simple, subumbellate racemes, 4–6 cm. long, with 1 or 2 slender, simple, secondary inflorescences usually being produced from the nodes of the primary scape. Flowers of moderate size for the genus, on spreading, filiform pedicels subtended by lanceolate, acute or acuminate, papery bracts. Sepals free, subequal, the dorsal sepal linear-lanceolate, acuminate, about 10 mm. long and 1.5 mm. wide, the lateral sepals rather obliquely linear-lanceolate, acuminate, about 12–13 mm. long and 0.6–1 mm. wide. Petals obliquely lanceolate, acuminate, about 10 mm. long and 1.2 mm. wide. Lip with an elongate basal claw, about 4 mm. long, the middle with a biauriculate thickening, the anterior margin of which is papillose-pubescent, the blade of the lip abruptly dilated, cordate-hastate, acuminate, about 4 mm. long and 2 mm. wide, the retrorse lateral lobes distinctly serrulate. Column slender, terete, about 3 mm. long, typical of the genus.

Panama and Costa Rica.

Bocas del Toro: Mosquito Hill, *Woodson, Allen & Seibert 1932.*

Apparently closely allied to *Notylia Wullschlaegeliana* Focke. Known only from the type collection and a single subsequent collection from the Dulce Golfo region in Costa Rica.

3. Notylia latilabia A. & S. in Sched. Orch. 8:71. 1925.

Epiphytic herbs unusually large for the genus, up to about 25 cm. tall, with short, oblong-complanate, striate-rugose, monophyllous pseudobulbs up to about 1.5 cm. long and 0.8 cm. wide, completely concealed by the large ovate-lanceolate, papery bracts which become fibrous with age. Leaves oblong-lanceolate to elliptic-lanceolate, subacute, coriaceous, up to about 20 cm. long and 4–5 cm. wide, contracted below into short, conduplicate petioles. Infloresences 1 or 2 arching or pendulous, densely flowered racemes 13–21 cm. long, produced from

the base of the current pseudobulb. Flowers relatively large for the genus, on slender pedicels subtended by narrowly triangular, acuminate bracts. Sepals concave, orange, the dorsal sepal free, fornicate, oblong-lanceolate, acute when flattened out, about 9–10 mm. long and 2.3–3 mm. wide, the lateral sepals connate to nearly the apex, forming a single bifid segment below the lip, about 8–9 mm. long and 4 mm. wide when spread out, the apices strongly reflexed. Petals falcately linear-ligular, acute, entirely white, antrorsely incurving in natural position, the apices deflexed, 7.6–8.4 mm. long and about 1.6 mm. wide. Lip shortly clawed at the base and obliquely inserted on the base of the column, the blade broadly trulliform, 6.3–7.1 mm. long (including the claw) and 4–5 mm. wide, the abruptly acuminate apex strongly recurved in natural position, the disk with a low carinate callus. Column slender, terete, glabrous, about 4.9 mm. long, typical of the genus.

Panama.

CANAL ZONE: Frijoles, sea level, *Powell 406*.

Reminiscent of *Notylia Barkeri*, but differing in the larger vegetative habit and much broader lip.

4. NOTYLIA PANAMENSIS Ames, Orchidaceae 7:112. 1922.

Epiphytic herbs rather large for the genus, up to about 18 cm. tall, with oblong, compressed, monophyllous pseudobulbs about 2 cm. long and 1 cm. wide, partially enveloped in the papery imbricating bracts which apparently soon weather away. Leaves oblong-lanceolate, obtuse and unequally bilobulate, coriaceous, up to 15 cm. long and 3–3.5 cm. wide, contracted below into very short, conduplicate petioles. Inflorescences pendulous, densely flowered racemes up to about 20 cm. long, produced from the base of the current pseudobulb. Flowers relatively large for the genus, white, on slender pedicels subtended by scarious, narrowly triangular, acuminate bracts. Sepals spreading, the dorsal sepal broadly elliptic-oblanceolate, obtuse, concave, about 7 mm. long and 5 mm. wide, the lateral sepals connate to the apex, forming a single linear-lanceolate segment below the lip, about 8 mm. long and about 2 mm. wide. Petals elliptic-lanceolate, acute, about 7 mm. long and up to 2.5 mm. wide. Lip clawed at the base, obliquely inserted on the base of the column, the blade sagittate, about 6 mm. long (including the claw) and 3 mm. wide across the base, the disk with a short, carinate callus. Column slender, terete, glabrous, about 3 mm. long.

Panama.

DARIÉN: Marragantí and vicinity, 10–200 ft., *R. S. Williams 977*.

A very distinctive species by reason of the broadly elliptic-obovate, obtuse dorsal sepal. Known only from the type collection.

5. NOTYLIA PENTACHNE Rchb. f. in Bonplandia 2:90. 1854.

Notylia gracilispica Schltr. in Fedde Rep. Sp. Nov. Beih. 17:75. 1922.

Epiphytic herbs of variable size, up to about 25 cm. tall, with oblong, compressed, monophyllous pseudobulbs up to about 2.5 cm. long and 1.2 cm. wide, usually partially enveloped in the conduplicate bases of the foliaceous bracts. Leaves and bract blades oblong-lanceolate to ligular, obtuse to subacute, coriaceous, up to about 20 cm. long and 2–5 cm. wide, contracted below into short conduplicate petioles. Inflorescences 1 or 2, usually elongate, slender, pendulous, many-flowered racemes up to about 35 cm. long, produced from the base of the current pseudobulb. Flowers of moderate size for the genus, on filiform pedicels subtended by inconspicuous linear-lanceolate, acuminate bracts. Sepals pale green, concave, the dorsal sepal lanceolate, acuminate, 8–10 mm. long and about 2–2.5 mm. wide, the apex slightly recurved, the lateral sepals connate for more than half their length, forming a single bifid segment below the lip, about 10 mm. long and 2.5 mm. wide, the subfalcate, acuminate apices divergently spreading and retrorse in natural position. Petals about 8 mm. long and 1.5 mm. wide, rather obliquely lanceolate, shortly acuminate, white with 2 minute orange spots in the center. Lip with an elongate, slender basal claw, the blade abruptly dilated and trulliform, acuminate, white, about 6 mm. long (with the claw) and up to about 2 mm. wide at the base, the disk with a short, carinate callus. Column slender, terete, distinctly papillose, about 5 mm. long.

Panama.

CANAL ZONE: along Río Chagres between Gamboa and Alajuela, 30–60 m., *Allen 961;* vicinity Gamboa, *Allen 3926, Pittier 2610;* Las Cruces, *Powell 3130,* Frijoles, *Powell 3318;* hills east of Panama City, *Powell 185, 3230.* VERAGUAS: Santa Fé, about 2500 ft., *Powell 400.*

A common lowland species, closely allied to the widespread *N. Barkeri,* but differing in the papillose column.

84. MACRADENIA R. Br.

MACRADENIA R. Br. in Bot. Reg. 8: *t. 612.* 1822; Benth. & Hook. Gen. Pl. 3:586. 1883.

Rhynchadenia A. Rich. in Sagra, Hist. Fis., Pol. y Nat. Cuba 12 (Fl. Cub. Fanerog. 2):248, *t. 85.* 1853.
Serrastylis Rolfe, in Gard. Chron. 16:726. 1894.

Small, epiphytic, pseudobulbose herbs, the plants reminiscent of a *Notylia* in habit. Leaves flat, ligular to lanceolate, fleshy or coriaceous. Inflorescences nodding or pendulous racemes, produced from the base of the current pseudobulb. Flowers of moderate size or sometimes rather small, on slender pedicels subtended by small bracts. Sepals subequal, free, more or less spreading. Petals similar to the sepals or a little smaller. Lip continuous with the base of the column, erect, deeply 3-lobed, the lateral lobes rather broad, erect, embracing the column, the mid-lobe spreading. Column erect, subterete, wingless, footless, the apex sulcate, the rostellum slender, erect or slightly inclined, the clinandrium broadly cupulate, with fimbriate or dentate margins. Anther erect at the base of

the clinandrium, oblong, imperfectly 2-celled, produced into a long appendage embracing the rostellum; pollinia 2, waxy.

A small genus of tropical American epiphytes, ranging from Florida and the West Indies to Mexico, Peru, and Brazil. One species is known from Panama.

1. MACRADENIA BRASAVOLAE Rchb. f. in Bot. Zeit. 10:734. 1852.

Epiphytic herbs with narrowly linear to oblong, compressed, monophyllous pseudobulbs 2.5–4.5 cm. long and 0.4–1.0 cm. wide, enveloped below in a few imbricating, papery bracts which soon weather away. Leaves ligular, acute, coriaceous, 6.5–16 cm. long and 1.2–2.2 cm. wide, contracted below into short, slender, conduplicate petioles. Inflorescences usually solitary, arching or pendulous, many-flowered racemes up to about 25 cm. long, but often less. Flowers of moderate size, on slender pedicels, subtended by inconspicuous, linear-lanceolate, acuminate bracts. Sepals subequal, free, spreading, reddish brown with translucent green margins, the dorsal sepal lanceolate, acuminate, concave, about 18 mm. long and 5 mm. wide, the laterals linear-lanceolate, acuminate, about 20 mm. long and 4 mm. wide, the reverse surfaces with a low central keel. Petals narrower than the sepals, reddish brown with translucent green margins, linear-lanceolate, acuminate, about 16 mm. long and 3.5 mm. wide. Lip conspicuously 3-lobed, about 12–15 mm. long and 7 mm. wide when spread out, contracted at the base and continuous with the base of the column, the lateral lobes semi-orbicular, white, erect, and embracing the column in natural position, the obliquely subacute anterior margins reflexed, the mid-lobe reddish brown, narrowly linear, acuminate, about 9 mm. long and 1 mm. wide, the disk with a low, fleshy, linear-oblong, obscurely striate callus. Column 6–7 mm. long, subterete, narrowed below, gradually dilated above, the margins of the clinandrium conspicuously lacerate, the rostellum narrowly linear-acuminate.

Guatemala, Nicaragua, Panama, Colombia, and probably adjacent territories.

PANAMÁ: hills east of Panama City, vicinity Juan Díaz, *Powell 3491, 3501;* without definite locality, *Fairchild s. n.;* vicinity Pacora, *Allen 2357.*

85. TELIPOGON HBK.

TELIPOGON HBK. Nov. Gen. & Spec. 1:335, *t. 75.* 1815; Benth. & Hook. Gen. Pl. 3:587. 1883; Kränzl. in Ann. Nat. Hist. Hofmus. Wien 33:9. 1919.

Telopogon Mutis, ex Spreng. Anleit. 2^1:291. 1817.
Thelypogon Spreng. Syst. Veg. 3:742. 1826.

Epiphytic herbs without pseudobulbs, the foliaceous stems short or elongate. Leaves usually narrow, distichous, congested or relatively distant, the blades articulated to the conduplicate bases, often deciduous, pergameneous, coriaceous or fleshy. Inflorescences slender, erect, few-flowered, pseudoterminal racemes produced from the uppermost leaf axils and usually exceeding the leaves in length. Flowers usually large in relation to the size of the plant, rarely small, on slender

pedicels subtended by small, inconspicuous bracts. Sepals subequal, free, broadly spreading, narrow, usually almost completely hidden by the petals and lip. Petals very broad, spreading, much exceeding the sepals in width, distinctly veined. Lip sessile at the base, broadly spreading, usually undivided, similar to the petals or a little broader, rarely smaller, prominently radiate or reticulate-veined. Column very short, stout, wingless, footless, densely setose or hispid on all sides or sometimes only at the apex, the rostellum terminal, erect, usually prominent. Anther erect, applied to the rostellum, distinctly 2-celled; pollinia 4, waxy.

Perhaps 60 species of small, tropical highland epiphytes, ranging from Costa Rica to Brazil and Peru. Two species are known from Panama.

a. Lip more than 2 cm. wide, radiate-veined, without secondary transverse nerves ..... 2. T. RADIATUS
aa. Lip less than 2 cm. wide, reticulate-veined, with distinct secondary transverse nerves ..... 1. T. DENDRITICUS

1. TELIPOGON DENDRITICUS Rchb. f. Otia Bot. Hamb. 1:6. 1878.

Dwarf, epiphytic herbs with short foliaceous stems 3 cm. tall (in our specimen). Leaves linear-lanceolate, acute, subcoriaceous, the blades 1.5–2 cm. long and 0.25–0.3 cm. wide, contracted below into a short, sheathing petiole. Inflorescences 1- to 2-flowered scapes up to about 6 cm. long, produced from the subterminal leaf axils. Flowers in our specimen about 2.5 cm. in diameter, pale greenish yellow, veined brown. Sepals narrowly triangular, acuminate, apparently 3-nerved, about 1 cm. long and 0.3 cm. wide. Petals incomplete in our specimen, apparently broadly rhombic, 9-nerved, probably about 1.2 cm. long and 1.2 cm. wide. Lip similar to the petals, transversely rhombic-ovate, obtuse, minutely apiculate, about 1.5 cm. long and 1.9 cm. wide, distinctly reticulate-veined, apparently with 19 primary veins and many secondary transverse nervules, the disk minutely puberulent. Column densely setose, the slender rostellum prominently projecting, as in the genus.

Panama and Colombia.

CHIRIQUÍ: vicinity Bajo Chorro, headwaters of the Río Caldera, 1900 m., *Woodson & Schery 694.*

The vegetative portion of our single specimen is very small, but the flower, although lacking the apices of the petals, seems to compare very well with the type description. The species apparently is allied to *Telipogon parvulus* of Costa Rica, but differs in the larger flowers and the distinct reticulate venation of the lip.

2. TELIPOGON RADIATUS Rchb. f. in Linnaea 41:70. 1877.

Dwarf, caespitose, epiphytic herbs, the distichous, congested, foliaceous stems 3.5–8 cm. tall. Leaves elliptic-lanceolate to ligular, acute, subcoriaceous, the blades 2–5.5 cm. long and 0.5–1 cm. wide, contracted below into short, conduplicate, imbricating petioles. Inflorescences 1 or 2 slender, erect, few-flowered racemes up to about 9 cm. long, produced from the subterminal leaf axils. Flowers averaging about 3.5 cm. in diameter, golden yellow striped with rich brown,

the elongate, slender pedicels subtended by very short, inconspicuous, narrowly triangular bracts. Sepals narrowly triangular, acuminate, 3-nerved, 1.2–1.5 cm. long and 0.35–0.4 cm. wide, the central nerves thickened and carinate on the outer surfaces. Petals broadly rhombic-ovate, shortly and distinctly acute, much exceeding the sepals in width, 9- to 11-nerved, 2–2.5 cm. long and 1.8–2.1 cm. wide. Lip subequal to the petals, the sessile base adnate to the base of the column, the blade transversely rhombic-ovate, obtuse, minutely apiculate, 19- to 21-nerved, the nerves radiate without secondary transverse nervules, about 2 cm. long and 2.2–2.7 cm. wide, the disk with a short, rounded, densely pilose callus. Column about 5 mm. long, densely setose, the slender rostellum prominently projecting.

Panama, Colombia, and Peru.

CHIRIQUÍ: vicinity Casita Alta, Finca Lérida, eastern slopes of Chiriquí Volcano, 1500–2000 m., *Woodson, Allen & Seibert 961*.

Our specimens differ from the combined concepts of Reichenbach f. and Kränzlin in the slightly smaller, apiculate lip, but otherwise appear to be identical. Evidently closely allied to *Telipogon ampliflorus* C. Schweinf. of Costa Rica, but differing in the radiate, rather than reticulate, venation of the lip and in the much more densely setose column.

86. DICHAEA Lindl.

DICHAEA Lindl. Gen. & Spec. Orch. Pl. 208. 1833; Benth. & Hook. Gen. Pl. 3:556. 1883; Kränzl. in Engler, Pflanzenr. IV, Fam. 50 (Heft 83):33 1923.

Fernandezia R. & P. Fl. Peru & Chil. Prodr. 123. 1794 (in part).
Epithecia Knowl. & Westc. Fl. Cab. 2:167, *t. 87*. 1838.
Epithecium Benth. & Hook. Gen. Pl. 3:529, 1239. 1883, sphalm.
Dichaeopsis Pfitz. in Engler & Prantl, Pflanzenfam. 2^6:207. 1888.

Epiphytic herbs without pseudobulbs, the erect or pendulous, monopodial, foliaceous stems enveloped in the conduplicate, distichously imbricating leaf bases. Leaf blades short to elongate, pergameneous to coriaceous, articulated and ultimately deciduous, or connate with the sheathing bases and persistent. Inflorescences 1 to several short, 1-flowered scapes produced from the axils of the leaves. Flowers relatively small. Sepals subequal, free, spreading, the laterals rather obliquely inserted, the bases sometimes forming a mentum with the column foot. Petals subequal to the sepals or narrower. Lip affixed to the base of the column, usually clawed, rarely sessile, the blade usually 3-lobed, often more or less anchoraeform when spread out, infrequently entire, the lateral lobes (if present) triangular to linear, short or elongate, usually retrorse in natural position, sometimes reduced to acute angular projections at the base of the blade, the disk usually without a callus. Column short, erect, wingless or rarely narrowly winged, the margins of the clinandrium often denticulate, the under-surface of the column sometimes with a glabrous or pubescent infra-stigmatic ligule, the base of the column produced into a short foot. Capsule ovoid or oblong, muricate, setose or smooth.

A difficult genus of tropical American epiphytes, ranging from Mexico and the West Indies to Brazil and Peru. Five species are known to occur in Panama.

a. Leaf blades not articulated, not deciduous.
  b. Leaf margins densely ciliate ..... 1. D. CILIOLATA
  bb. Leaf margins not ciliate ..... 3. D. MURICATA
aa. Leaf blades articulated to the sheathing bases, deciduous.
  b. Leaves broadly oblong-ligular, obtuse, minutely apiculate, 8 mm. wide or more ..... 2. D. MORRISII
  bb. Leaves narrowly linear-lanceolate, acute or acuminate, 6 mm. wide or less.
    c. Leaves 4 cm. long or less, usually of alternating groups of unequal length ..... 4. D. PANAMENSIS
    cc. Leaves more than 6 cm. long, all of about equal length ..... 5. D. POWELLII

1. DICHAEA CILIOLATA Rolfe, in Kew Bull. 83. 1917.

Small, epiphytic herbs, the distichous, often branching, densely foliaceous stems up to about 15 cm. tall and 8–10 mm. wide. Leaf blades elliptic-oblong, acute, distinctly keeled below, the margins densely ciliate, 2.5–3 mm. long and 2.5–3 mm. wide at the base, the blades not articulated to the sheathing bases, not deciduous. Inflorescences slender, 1-flowered scapes 4–6 mm. long, produced from the upper leaf axils, the apex with 2 short, spathaceous bracts enveloping the ovary. Flowers small, the sepals and petals pale buff with red-purple spots and bars, the lip white marked with purple. Sepals free, the dorsal sepal oblong, acute, 5.5–7 mm. long and about 2 mm. wide, the lateral sepals ovate, acute to shortly acuminate, rather concave at the base, 6–8 mm. long and 2–3 mm. wide, the outer surfaces of the sepals sparsely verrucose. Petals rather obliquely elliptic-lanceolate, acute, about 7 mm. long and 3 mm. wide. Lip shortly clawed at the base, the claw more or less geniculate in profile and continuous with the base of the column, the blade anchoraeform when spread out, 3-lobed, the narrowly linear, subfalcate, lateral lobes retrorsely incurving, the mid-lobe triangular, broadly acute, the lateral margins more or less erect in natural position, the entire lip (including the claw) about 4.5–6.4 mm. long and 6–8 mm. wide. Column rather stout, wingless, 3–5 mm. long, the lower surface with a short infra-stigmatic ligule. Capsule densely muricate.

Costa Rica and Panama.

CHIRIQUÍ: without definite locality, 4000 ft., *Powell 435*.

This concept is very closely allied to that of *Dichaea hystricina* Rchb. f. and may ultimately prove to be conspecific.

2. DICHAEA MORRISII Fawcett & Rendle, in Jour. Bot. 48:107. 1910.

Epithecia Morrisii Schltr. in Orchis 9:26. 1915.
Dichaea Bradeorum Schltr. in Fedde Rep. Sp. Nov. Beih. 19:154. 1923.

Epiphytic herbs, the erect or pendulous stems up to about 40 cm. tall, enveloped in the very broad, conduplicate bases of the distichously imbricating leaves, the plants superficially resembling some of the pseudobulbless Maxillarias. Leaf blades articulated to the sheathing bases and ultimately deciduous below,

elliptic-oblong to broadly ligular, obtuse and minutely apiculate, subcoriaceous, 3–7 cm. long and 0.8–1.5 cm. wide. Inflorescences 1-flowered scapes, about 8 mm. long, produced from the upper leaf axils, the peduncle provided at the apex with 2 large spathaceous bracts which completely envelop and conspicuously exceed the ovary. Flowers large for the genus, the sepals and petals pale green striped deep lavender, the lip deep lavender. Sepals lanceolate, acuminate, slightly concave, the margins minutely ciliate, about 11–15 mm. long and 5–7 mm. wide, the lateral sepals rather oblique and a little broader than the dorsal sepal, with a rather indistinct central keel on the outer surface. Petals subequal to the dorsal sepal, lanceolate, acuminate, slightly concave, about 10–12 mm. long and 3.5–4 mm. wide, the margins minutely ciliate. Lip fleshy, the linear-oblong, slightly arcuate claw narrowed at the base and affixed to the very short column foot, the blade dilated and 3–lobed, more or less anchoraeform, the lateral lobes short to elongate, ligular to subular, sometimes falcately triangular-linear, usually more or less retrorse in natural position, the mid-lobe rather narrowly triangular, usually reflexed, acute or shortly acuminate, minutely papillose on both sufaces, the entire lip (including the claw) about 9–10 mm. long and 5–6 mm. wide. Column very stout, the lateral margins narrowly winged, 4–6 mm. long, the clinandrium very broad, with serrulate margins, the under-surface of the column with a subquadrate, puberulent, slightly emarginate, infra-stigmatic ligule, the base of the column produced into a very short foot. Capsule densely setose.

Jamaica, Santo Domingo, Costa Rica, and Panama.

COCLÉ: hills north of El Valle de Antón, 1000 m., *Allen 2874*. CHIRIQUÍ: vicinity Bajo Chorro, 6000 ft., *Davidson 221*.

Apparently a very variable species. The collection cited above from El Valle de Antón is rather atypical in the narrower leaves and the much reduced lateral lobes of the lip.

3. DICHAEA MURICATA (Sw.) Lindl. Gen. & Sp. Orch. Pl. 209. 1833.

Cymbidium muricatum Sw. in Nov. Act. Soc. Upsal. 6:71. 1799.
Dichaea latifolia Lindl. Gen. & Sp. Orch. Pl. 208. 1833.
Dichaea Moritzii Rchb. f. in Nederl. Kruidk. Arch. 4:328. 1858.
Dichaea muricata Lindl. *β latifolia* Lindl. ex Griseb. Fl. Brit. W. Ind. 624. 1864.
Dichaea muricata Lindl. var. *Moritzii* Cogn. in Mart. Fl. Bras. 3^6:488. 1906.
Dichaea ovatipetala Schltr. in Fedde Rep. Sp. Nov. Beih. 19:266. 1923.
Dichaea similis Schltr. loc. cit. 307. 1923.
Dichaea verrucosa Ames & Schweinf. in Sched. Orch. 8:83. 1925.

Epiphytic herbs with elongate, pendulous, monopodial, foliaceous stems, up to about 60 cm. long, completely enveloped in the persistent, distichous leaves. Leaf blades elliptic-oblong to ligular, obtuse to acute, with entire margins, the under-surface distinctly keeled, terminating at the apex in a minute to relatively elongate apicule, the blades often rather obliquely spreading, not articulated to the sheathing bases, not deciduous, 10–20 mm. long and 4–7 mm. wide. Peduncles slender, 1-flowered, 1–2 cm. long, produced from the upper leaf axils. Flowers of moderate size for the genus. Sepals elliptic-lanceolate,

shortly acuminate, about 7.5 mm. long, 2.5 mm. wide, the outer surfaces usually more or less verrucose. Petals subequal to the sepals, elliptic-lanceolate, acute to shortly acuminate, about 7 mm. long and 2 mm. wide. Lip anchoraeform in outline when spread out, the broad claw contracted at the base and affixed to the base of the column, the blade abruptly dilated and distinctly 3-lobed, the short, acute or acuminate lateral lobes more or less falcately retrorse in natural position, the mid-lobe shortly triangular, acute or apiculate, the entire lip, including the claw, about 6 mm. long and 3.2 mm. wide. Column stout, about 2.5–3 mm. long, the under-surface with a small infra-stigmatic ligule, the broad clinandrium hooded, as in the genus. Capsule densely muricate.

Mexico to Brazil; Cuba to Lesser Antilles.

COLÓN: summit of Cerro Santa Rita, 1200–1500 ft., *Allen & Allen 5112*. COCLÉ: western slope and summit of Cerro Valle Chiquito, 700–800 m., *Seibert 512;* vicinity El Valle de Antón, 600–1000 m., *Allen 1249*. CHIRIQUÍ: vicinity Casita Alta, Finca Lérida, eastern slopes of Chiriquí Volcano, 1500–2000 m., *Woodson, Allen & Seibert 834;* vicinity Cerro Punta, headwaters of the Río Chiriquí Viejo, 2000 m., *Allen 1529*.

Most of the specimens cited above are sterile, and the determinations must be regarded as provisional. In particular, the collections from Chiriquí Province appear quite atypical in the narrower leaves and may possibly represent *Dichaea trichocarpa* (Sw.) Lindl.

4. DICHAEA PANAMENSIS Lindl. Gen. & Sp. Orch. Pl. 209. 1833.

Epithecia panamensis Schltr. in Orchis 9:25. 1915.
Dichaeopsis panamensis (Lindl.) Schltr. in Beih. Bot. Centralbl. 36^2:519. 1918.

Epiphytic herbs with slender, monopodial, often rather flexuose foliaceous stems, 4 to about 18 cm. tall. Leaves 2-ranked on the stems, narrowly linear-lanceolate, acute and apiculate or acuminate, subcoriaceous, often glaucous, usually in alternating groups of unequal length, the blades articulated to the sheathing bases and ultimately deciduous below, 1–4 cm. long and 0.2–0.45 cm. wide. Peduncles filiform, 1-flowered, produced from the axils of the leaves. Flowers small, translucent, white spotted with pink or purple. Sepals free, the dorsal sepal oblong-lanceolate, acute, slightly concave, about 5 mm. long and 2 mm. wide, the lateral sepals obliquely oblong-lanceolate, acute, slightly concave, about 6 mm. long and about 2.5 mm. wide at the base. Petals shorter and broader than the sepals, rather obliquely elliptic-oblong, shortly acute, about 4.5 mm. long and 3.5 mm. wide. Lip sagittate to obovate-spatulate in outline when spread out, the ligular claw slightly arcuate in profile, abruptly contracted at the base and continuous with the short column foot, the blade abruptly dilated and 3-lobed, the short, acute lateral lobes retrorse in natural position, the mid-lobe broadly triangular, shortly acute with a short central keel on the lower surface at the apex, the entire lip, including the claw, about 7 mm. long and 6 mm. wide. Column wingless, stout, about 3 mm. long, the apex truncate, the under-surface with a short, infra-stigmatic ligule, the base produced into a very short foot. Anther and pollinia typical of the genus.

Fig. 212. *Dichaea panamensis*

Mexico, British Honduras, Guatemala, Honduras, Costa Rica, and Panama.

CANAL ZONE: hills between Rio Grande and Puerto Vidal, on the road to Arraiján, 50–150 m., *Pittier 2716;* Barro Colorado Island, Gatún Lake, 100 m., *Wetmore & Abbe 249;* Miraflores, *Powell 3133;* Pedro Miguel, *Powell 3033;* Río Indío, Madden Lake area, 70–80 m., *Dodge & Allen 17312;* Chagres, *Fendler 333.* PANAMÁ: without definite locality, *Cuming 1292;* low thick scrub along the Río Tecúmen, north of the Chepo road, about 30 m., *Hunter & Allen 221;* Chiva-Chiva, *Powell 3021, 3066;* Río Tapía, *Standley 30671;* hills east of Panama City, *Powell 175;* vicinity Paja, *Powell 3139, 3240;* Chorrera, *Powell 3078;* Panama Bay, Perlas Archipelago, San José Island, *Johnston 400, 1013, 1216, 1219.* COCLÉ: Bismarck, above Penonomé, 2000–3000 ft., *R. S. Williams 441;* vicinity El Valle de Antón, 600–1000 m., *Fairchild s. n., Allen 1246.*

A very common lowland species, widely distributed in Central America.

5. DICHAEA POWELLII Schltr. in Fedde Rep. Sp. Nov. Beih. 17:90. 1922.

Dichaea Brenesii Schltr. loc. cit. 19:264. 1923.

Erect, epiphytic herbs with unbranching, monopodial, foliaceous stems 15–45 cm. tall, enveloped in the conduplicate bases of the many, distichously imbricating leaves. Leaf blades spreading, linear-ligular, acute to acuminate, coriaceous, 6–13.5 cm. long and 0.3–0.6 cm. wide, the blades articulated to the persistent sheathing bases and ultimately deciduous below. Inflorescences short, slender, 1-flowered scapes about 1.5–2 cm. long, produced from the leaf axils, terminating at the apex in a short, broadly cucullate bract which envelops and exceeds the ovary. Flowers relatively large for the genus, the sepals and petals pale green to white, the lip purple or pale green heavily marked with purple. Sepals free, glabrous, ovate-lanceolate to oblong-lanceolate, acute, 8–10 mm. long and 4 mm. wide. Petals elliptic-ovate, obtuse and apiculate to shortly acute, slightly concave, about 10 mm. long and 4 mm. wide. Lip with a broad ligular claw at the base, the blade dilated and 3-lobed, broadly trulliform when spread out, deeply concave in natural position, the short, obtuse to acute lateral lobes somewhat retrorse, the mid-lobe semi-orbicular when spread out, more or less conduplicate and shortly acute in natural position, the entire lip, including the claw, about 8 mm. long and 8 mm. wide. Column broad, stout, about 4–6 mm. long, the under-surface with a short, minutely papillose, infra-stigmatic ligule. Capsule glabrous.

Honduras, Costa Rica, and Panama.

PANAMÁ: foothills east of Panama City, *Powell 23.* COLÓN: Cerro Santa Rita, 1200 ft., *Allen & Fairchild 5186, 5193.*

87. CAMPYLOCENTRUM Benth.

CAMPYLOCENTRUM Benth. in Jour. Linn. Soc. 18:337. 1881; Benth. & Hook. Gen. Pl. 3:585. 1883 (as *Campylocentron*).

Todaroa A. Rich. in Ann. Sci. Nat. III, 3:28. 1845.

Pseudobulbless, epiphytic herbs with either distichous, monopodial, leafy stems, or stemless and leafless clusters of thickened roots. Leaves oblong or ligular, coriaceous, sometimes absent. Inflorescences short, usually densely flowered racemes, produced from the axils of the leaves or from the centers of the root clusters. Flowers minute, often more or less distichously arranged on the scape. Sepals subequal, free, connivent, or with the apices spreading. Petals subequal to the sepals or sometimes smaller. Lip sessile at the base of the column and produced into an elongate, often recurved spur, the blade entire or 3-lobed, subequal to the sepals in length, often with the lateral margins more or less convolute at the base. Column very short, wingless, the base without a foot. Anther terminal, operculate, incumbent, 2-celled; pollinia 2, waxy.

About 30 species of tropical American epiphytes, ranging from Florida, Mexico, and the West Indies to Brazil. Three species are known from Panama, but one is represented only by sterile material.

a. Plants entirely leafless, consisting of spreading clusters of thickened roots..... 3. C. sp.
aa. Plants with monopodial, foliaceous stems.
  b. Leaves less than 1.5 cm. long. Highland species..... 1. C. Brenesii
  bb. Leaves 4–9 cm. long. Lowland species..... 2. C. micranthum

1. Campylocentrum Brenesii Schltr. in Fedde Rep. Sp. Nov. Beih. 19:268. 1923.

Small, epiphytic herbs with erect, distichous, monopodial, foliaceous stems 2–12 cm. tall. Leaves spreading, the blades oblong to elliptic-oblong, rather obliquely acute, coriaceous, about 7–14 mm. long and 3.5–5 mm. wide, articulated to the sheathing bases and ultimately deciduous below. Inflorescences short, lateral, 5–10-flowered racemes produced from the leaf axils. Flowers minute, distichously arranged on the scape. Sepals narrowly lanceolate-ligular, acute, about 1.75 mm. long, the laterals usually rather oblique. Petals subequal to the sepals, rather obliquely linear-lanceolate, acute. Lip 3-lobed, about 1.75 mm. long and 1 mm. wide, the lateral lobes short, obtuse, the mid-lobe narrowly triangular, the base produced into a somewhat laterally compressed, obtuse spur about 1 mm. long. Column very short, typical of the genus.

Guatemala, Costa Rica, and Panama.

chiriquí: vicinity Bajo Mono and Quebrada Chiquero, 1500 m., *Woodson & Schery 579*.

2. Campylocentrum micranthum (Lindl.) Rolfe in Orch. Rev. 11:245. 1903.

Angraecum micranthum Lindl. in Bot. Reg. 21: *t. 1772*. 1836.
Angraecum brevifolium Lindl. loc. cit. n. s. 3: sub *t. 68*. 1840.
Angraecum Lansbergii Reichb. f. in Nederl. Kruidk. Arch. 4:316. 1859.
Aeranthus micranthus Reichb. f. in Walp. Ann. 6:901. 1864.
Aeranthus Lansbergii Reichb. f. loc. cit. 1864.
Campylocentrum panamense Ames, Orchidaceae 7:88. 1922.
Campylocentrum peniculus Schltr. in Fedde Rep. Sp. Nov. Beih. 17:91. 1922.

Fig. 213. *Campylocentrum micranthum*

Epiphytic herbs, with more or less flexuose, monopodial, foliaceous stems, up to about 35 cm. long, enveloped in the conduplicate bases of the distichous leaves. Roots alternating with the leaves and equidistantly distributed along the stem. Leaves broadly ligular to elliptic-oblong, obtuse to unequally bilobed at the apex, the blades about 4–9 cm. long and 1.2–2 cm. wide, articulated to the persistent, sheathing bases and ultimately deciduous below. Inflorescences short, lateral, densely flowered racemes 3–4 cm. long, produced from the sides of the stems just below the point of emergence of the roots. Flowers very small, white or yellowish white, distichously arranged on the scape. Sepals of about equal length, linear-ligular, shortly acuminate, slightly concave, the margins of the lower portions connivent, with the apices spreading, 4–4.5 mm. long and about 0.75 mm. wide; lateral sepals usually rather oblique. Petals narrowly ligular, rather concave, acute, subequal to the dorsal sepal in length, about 4 mm. long and 0.75–1 mm. wide. Lip 3-lobed, about equaling the lateral sepals in length, the sessile base affixed to the base of the column and produced into an elongate, obtuse, incurving spur, about 4 mm. long, the short, lateral lobes of the blade acute or semiovate, erect in natural position, about 1.5 mm. wide when spread out, the mid-lobe narrowly triangular or linear-ligular, rather acute, about 2.5 mm. long and 0.75 mm. wide.

Cuba, Santo Domingo, Jamaica, Trinidad, Mexico to British Guiana, Brazil and Peru.

CANAL ZONE: Las Cascadas, *Powell 184, Standley 25748, 29699;* drowned forest near Vigía and San Juan de Pequení, Madden Lake area, 66 m., *Dodge, Steyermark & Allen 16582;* in woods, near Gatún, *Sutton Hayes 988;* vicinity Gamboa, 100 m., *Allen 3444, Pittier 2612.* BOCAS DEL TORO: Water Valley, vicinity Chiriquí Lagoon, *von Wedel 1386, 1451, 1483, 1655, 1707.*

3. CAMPYLOCENTRUM sp.

There is a specimen in the Ames Herbarium of a leafless species of *Campylocentrum* from Panama, the single inflorescence being very immature and without flowers. It seems likely that it represents *Campylocentrum fasciola* (Lindl.) Cogn. which is widely distributed from Mexico and the West Indies to Brazil.

PANAMÁ: hills east of Panama City, *Powell 320.*

INDEX TO PART III

(JUNCACEAE–ORCHIDACEAE)

Numbers represent italicized page numbers at bottom of pages. Synonyms in *italics*.

A

Abacá, *48*
Achroanthes, 234; mianthemifolia, 235; montana, 236
Acineta, *381;* chrysantha, *382; densa, 382; fulva, 382; Colmani, 382; Humboldtii, 382; sella-turcica, 382;* superba, *382; Warscewiczii, 382*
Acoidium, 475
Acostaea, *190;* costaricensis, *191*
Acropera, 395; armeniaca, 396; cornuta, 396
Adipe, 408
Aeranthus Lansbergii, 579; micranthus, 579
Agapanthus, *2*
Agave, *12, 14;* panamana, *14;* picta, *14*
Allen, Paul H., *337, 469*
Allium, *2*
Aloe, *2*
Alpinia, 57; aromatica, 59; exaltata, 62; jamaicensis, 59; multicaulis, 59; occidentalis, 59; Renealmia, 62; spicata, 71; spiralis, 69; tubulata, 62
Alstroemeria edulis, 17; hirsuta, 16
Amaryllidaceae, *12*
Amaryllis carnea, *22; longifolia* var. *longiflora, 20; nervosa, 22;* rosea, *22; tubispatha, 22*
Ames, Blanche, *337*
Ames, Oakes, *337*
Amphiglottis, 247
Androsolen, 36
Angraecum brevifolium, 579; Lansbergii, 579; micranthum, 579
Anguloa superba, 382
Anonymos capitatus, 43
Anthericum, *2; apodastanthum, 3;* echeandioides, *3;* macrophyllum, *3; panamense, 3*
Apteria, *46;* aphylla, *47; boliviana, 47; setacea, 47*
Arbol de Viájero, *48*
Arethusa picta, 156; racemosa, 150
Argyropsis, 21
Arrowroot, *81, 103*
Arviela, 21
Asparagus, 2
Aspasia, *499;* epidendroides, *501,* var. principissa, *501; fragrans, 501; principissa, 501;* pusilla, *503; Rousseauae, 501*
Asteranthemum, 5
Atamosco, 21
Auliza, 247; ciliaris, 257
Aurota, 19

B

Banana, *48*
Bandera española, *75*
Banksea, 63
Baptistonia, 514
Barkeria, 247
Batemannia Burtii, 429; grandiflora, 417
Bauxia, 35
Beef-steak Heliconia, *51*
Beloglottis, 152; costaricensis, 154
Benitzia, 44; suaveolens, 44
Bermudiana, 36
Bifrenaria, *408;* picta, *409*
Bihai, 48; aurantiaca, 56; barqueta, 51; Bihai, 51; Borinquena, 51; Champneiana, 51; choconiana, 55; densa, 50; elongata, 51; imbricata, 50; latispatha, 52; longa, 54; marginata, 54; platystachys, 54; punicea, 50; purpurea, 51; reticulata, 50; rostrata, 54; rutila, 51; straminea, 56; tortuosa, 53
Bihaia, 48; acuminata, 55; Bourgeauana, 51; cannoidea, 56; conferta, 50; curtispatha, 54; dasyantha, 53; elegans, 50; hirsuta, 56; Mariae, 50; pendula, 54; psittacorum, 56; vellerigera, 54; villosa, 53; Wagneriana, 50
Blephanthera, 2
Bletia, *339; capitata, 129; Lankesteri, 342; pallida, 340;* purpurea, *340;* reflexa, *342; verecunda, 340*
Bletiana, 339
Bletilla, 339
Bolbophyllaria, 344; aristata, 345; pachyrachis, 345
Bollea Wendlandiana, 421
Bomarea, *14;* Allenii, *16; Caldasiana* var. *concolor, 16;* chiriquina, *15;* chontalensis, *16;* edulis, *17; edulis* var. *chontalensis, 16;* hirsuta, *16,* var. concolor, *16*
Bonatea pauciflora, 120
Bothriochilus, *330;* macrostachyus, *330*
Brachystele, 152; aguacatensis, 153; guyanensis, 153

Brassavola, *316*; acaulis, *318*; *lineata*, *318*; nodosa, *316*; *scaposa*, *316*; *venosa*, *316*
Brassia, *505*; Allenii, *506*; caudata, *506*; chlorops, *509*; Gireoudiana, *510*; *Lawrenciana* var. *longissima*, *511*; *Lewisii*, *508*; longissima, *511*; *longissima*, *511*, var. *minor*, *508*; *parviflora*, *509*
Broughtonia alba, *436*
Bulbophyllum, *344*; aristatum, *345*; pachyrrhachis, *345*; *vinosum*, *345*
Burlingtonia, *478*
Burmannia, *43*; capitata, *43*
Burmanniaceae, *42*

C

Cabuya, *13*; blanca, *13*
Cadalvena, *63*
Café cimarron, *75*
Café silvestre, *75*
Calanthe, *337*; mexicana, *339*
Calathea, *82*; *albicans*, *94*; Allenii, *89*; Allouia, *86*, var. violacea, *89*; altissima, *94*; *Casupito*, *83*; chrysoleuca, *93*; *cylindrica*, *87*; *dasycarpa*, *96*; *discolor*, *83*; foliosa, *92*; *grandifolia*, *87*; *hirsuta*, *85*; indecora, *89*; insignis, *84*; lagunae, *89*; lasiostachya, *84*; *leucocephala*, *98*; *leucophaea*, *98*; lutea, *83*; *macrosepala*, *87*; *marantina*, *83*; *micans*, *94*; microcephala, *94*; panamensis, *92*; *pardina*, *85*; picta, *91*; *quadratispica*, *84*; villosa, *85*; Warscewiczii, *92*
Camaridium, *431*; *affine*, *442*; *arachnites*, *446*; *Biolleyi*, *439*; *Bradeorum*, *440*; *ctenostachys*, *446*; *dendrobioides*, *447*; *exaltatum*, *448*; *grandiflorum*, *440*; *Jimenezii*, *447*; *latifolium*, *460*; *minus*, *455*; *nutantiflorum*, *464*; *ochroleucum*, *442*; *simile*, *447*
Campylocentron, *578*
Campylocentrum, *578*; Brenesii, *579*; fasciola, *581*; micranthum, *579*; *panamense*, *579*; *peniculus*, *579*; sp., *581*
Caña de Mico, *64*
Cañagria, 64
Canna, *74*; *angustifolia*, *76*; *aurantiaca*, *75*; coccinea, *78*; *commutata*, *75*; *densiflora*, *75*; edulis, *78*; *elegans*, *76*; flaccida, *76*; *flava*, *76*; *floribunda*, *75*; glauca, *76*; indica, *77*; *indica* var. *patens*, *77*; liliiflora, *78*; *liturata*, *76*; lutea, *75*; *maculata*, *75*; *patens*, *77*; *Schlechtendaliana*, *76*; *stricta*, *76*; *sylvestris*, *77*; *Warscewiczii*, *78*
Cannaceae, *74*
Cannacorus, *74*; *indicus*, *77*; *ovatus*, *77*
Catachaetum, *359*
Catasetum, *358*; bicolor, *360*; *Brenesii*, *363*; eburneum, *362*; *gongoroides*, *360*; Oerstedii, *363*; *rostratum*, *363*; *scurra*, *367*; *serratum*, *365*; suave, *365*; viridiflavum, *365*; Warczewitzii, *367*
Cattleya, *312*; Skinneri var. autumnalis, *313*
Century Plant, *14*
Ceratochilus, *389*; *oculatus*, *391*
Chondrorhyncha, *419*, *427*; aromatica, *421*; caloglossa, *421*; costaricensis, *422*; discolor, *423*; *estrellensis*, *421*; lactea, *423*; *Lipscombiae*, *424*; marginata, *424*
Choretis, *24*
Chysis, *343*; aurea var. maculata, *343*
Cipura, *35*; *graminea*, *36*; *humilis*, *36*; paludosa, *36*
Cladobium, *318*
Cleistes, *123*; *rosea*, *123*
Clowesia, *359*
Coelia macrostachya, *330*, var. *genuina*, *331*, var. *integrilabia*, *331*
Coeliopsis, *376*; hyacinthosma, *377*
Coppensia, *514*
Coryanthes, *402*; *Albertinae*, *403*; *Hunteriana*, *403*; maculata, *403*; *Powellii*, *403*; *splendens*, *403*
Corymbis, *161*; *flava*, *161*
Corymborchis, *161*; *flava*, *161*
Corynanthes, *402*
Corythantes, *402*
Costus, *63*; *amazonicus*, *67*; Bakeri, *67*; *cernuus*, *58*; *conicus*, *71*; cylindricus, *71*; *formosus*, *69*; *Friedrichsenii*, *65*; *giganteus*, *67*; *hirsutus*, *64*; laevis, *67*; *laxus*, *67*; lima, *67*; *lima* var. *Wedelianus*, *67*; *Malortieanus* var. *amazonicus*, *67*; *maximus*, *67*; nutans, *71*; *Pisonis*, *69*; *podocephalus*, *58*; ruber, *69*; sanguineus, *69*; scaber, *72*; *Skutchii*, *67*; spicatus, *71*; *spicatus*, *69*, var. β *pubescens*, *64*; spiralis, *69*; *spiralis*, *69*; *splendens*, *67*; *uniflorus*, *73*; villosissimus, *64*; *Weberbaueri*, *67*
Craniches, *148*; muscosa, *148*; *oligantha*, *146*; *stachyodes*, *147*
Crinopsis, *19*
Crinum, *19*; *Commelini*, *20*; darienensis, *21*; erubescens, *20*; *Kunthianum*, *20*; longiflorum, *20*
Cryptocentrum, *472*; gracilipes, *473*; inaequisepalum, *473*; latifolium, *474*; Standleyi, *475*
Cryptophoranthus, *176*; *acaulis*, *208*; lepidotus, *178*; *Powellii*, *209*
Cryptosaccus, *546*
Cryptosanus, *546*; *scriptus*, *548*
Ctenanthe, *95*; *dasycarpa*, *96*
Cuculina, *358*
Cuitlanzina, *492*
Cuitlauzina, *492*

Cuitlauzinia, 492
Curculigo, *19;* scorzoneraefolia, *19*
Curcuma, *57; americana, 86*
Cybelion, 476
Cyclopogon, 152; Prasophyllum, 154
Cyclosia, 354
Cycnoches, *368; Amparoanum, 373;* aureum, *369; barbatum, 389;* chlorochilon, *370; densiflorum, 373;* Dianae, *372;* Egertonianum, *373; glanduliferum, 373; guttulatum, 373; pachydactylon, 373; pauciflorum, 373; peruvianum, 373; Powellii, 372; Rossianum, 373; stelliferum, 373; stenodactylon, 373;* Tonduzii, *374;* ventricosum, *376; ventricosum* var. *Egertonianum, 373; Warszewiczii, 370*
Cymbidium muricatum, 575; ochroleucum, 442; pusillum, 540; subulatum, 488; trinerve, 349; utriculatum, 353
Cymbocarpa, 44
Cypella caerulea, 35; gracilis, 35
Cypripedium caudatum, 116, var. *roseum, 116,* var. *Warscewiczii, 116; Hincksianum, 117; Humboldti, 116; longifolium, 117; Warszewiczianum, 116*
Cyrtochilos, 514
Cyrtochilum, 514
Cyrtopera, 347; longifolia, 347; Woodfordii, 347
Cyrtopodium, *349;* punctatum, *349,* var. *Saintlegerianum, 349; Saintlegerianum, 349; speciosissimum, 349; tigrinum, 349; Willmorei, 349; Woodfordii, 347*

D

Dendrobium album, 436; longifolium, 347; ruscifolium, 206; utricularioides, 478
Deppia, 410
Diacrium, *310;* bilamellatum, *312; bilamellatum* var. *Reichenbachianum, 312*
Dichaea, *573; Bradeorum, 574; Brenesii, 578;* ciliolata, *574; latifolia, 575; Moritzii, 575;* Morrisii, *574;* muricata, *575; muricata* var. *latifolia, 575,* var. *Moritzii, 575; ovatipetala, 575;* panamensis, *576;* Powellii, *578; similis, 575;* trichocarpa, *576; verrucosa, 575*
Dichaeopsis, 573; panamensis, 576
Dicrypta, 431; Baueri, 445; crassifolia, 445; iridifolia, 466; irisphyta, 466
Didactyle, 344
Dillon, Gordon W., *337*
Dimerandra, 247; stenopetala, 270
Dimerocostus, *72; strobilaceus, 73;* uniflorus, *73*
Dinema, 247; paleaceum, 256
Dioscorea, *26;* alata, *26; anconensis, 32; Billbergiana, 32;* borealis, *31;* bulbifera, *26; capillaris* var. *glabra, 30;* cayennensis, *26;* convolvulacea, *30; costaricensis, 28;* cymosula, *32; cymosula* var. *Duchassaingii, 32;* lepida, *30;* macrostachya, *32;* panamensis, *30; permollis, 32; pilosiuscula* var. *panamensis, 28;* polygonoides, *33;* racemosa, *31;* samydea, *29,* var. corcovadensis, *29;* sapindoides, *28;* Standleyi, *33;* trifida, *31;* urophylla, *29*
Dioscoreaceae, *26*
Diothonaea imbricata, 245; oppositifolia, 245
Distemon, 74
Dracaena, *2*

E

Echeandia, *4;* prolixa, *5;* venusta, *4*
Echeandiaea, 4
Echthronema, 36
Eckardia, 384
Elleanthus, *128;* aurantiacus, *130;* capitatus, *129;* hymenophorus, *129;* laxus, *132; linifolius, 132;* muscicola, *133; Tonduzii, 130; trilobatus, 130*
Encyclia, 247; atropurpurea, 255, var. *leucantha, 255,* var. *rhodoglossa, 255; Brenesii, 262; campylostalix, 256; chiriquensis, 269; gravida, 262; Hunteriana, 262; Powellii, 261; ramonensis, 261; tessalata, 259; Tonduziana, 262*
Endocodon, 82
Endogona, 2
Epidanthus, *335;* paranthicus, *336*
Epidendrum, *247; aberrans, 276;* abbreviatum, *254; Adolphi, 284; alanjense, 262; Allenii, 270; aloifolium, 264; amandum, 262;* anceps, *273;* atropurpureum, *255,* var. laciniatum, *255; auritum, 256; auropurpureum, 255; baculibulbum, 260; benignum, 290; biflorum, 301; bilamellatum, 312;* bisulcatum, *273; Boissierianum, 301;* Brassavolae, *256; brevicaule, 304;* Boothii, *255;* caligarium, *275;* campylostalix, *256; cardiophorum, 303;* Carolii, *276; carthaginense, 522; caudatum, 506;* centradenia, *276;* centropetalum, *276; chiriquense, 269; chlorocorymbos, 281; chondranthum, 285;* ciliare, *257,* var. Oerstedii, *259;* cochleatum, *259;* cocleense, *277; colonense, 306;* condylochilum, *259;* confertum, *277; congestoides, 304;* congestum, *278;* coriifolium, *278; coriifolium* var. *purpurascens, 278; costaricense, 259;* crassilabium, *260;* criniferum, *279;* cryptanthum, *279; curvicolumna, 281; cuspidatum, 257; Cycno-*

stalix 268; Deamii, 259; dentiferum, *279;* dentilobum, *281;* difforme, *281,* var. firmum, *283,* var. simulacrum, *283;* eburneum, *283;* ellipsophyllum, *284;* Endresii, *284; equitans, 285;* equitantifolium, *285;* exasperatum, *285; falcatum* var. *Zeladoniae, 264; firmum, 283; flexicaule, 301; floribundum, 293;* fragrans, *260,* var. *pachypus, 260; fuscopurpureum, 278; gibbosum, 295; gigas, 349, 519; glandulosum, 268; gravidum, 262; Hoffmannii, 261;* Hunterianum, *286;* ibaguense, *286;* imatophyllum, *287; imbricatum, 301,* var. *angustifolium, 301;* incomptum, *287;* ionophlebium, *261;* isomerum, *289; Isthmi, 293; labiatum, 547; latilabrum, 281; leprosum, 276;* lividum, *310;* lockhartioides, *289; lorifolium, 287; leucocardium, 283; macrochilum, 255,* var. *roseum, 255; magnibracteatum, 278; majale, 283;* microdendron, *289; modestiflorum, 301; Mooreanum, 262;* moyobambae, *290; musciferum, 273; myodes, 298;* nocturnum, *291,* var. *panamense, 291; nodosum, 316;* obesum, *292; Oerstedii, 259;* oncidioides var. gravidum, *262,* var. Mooreanum, *262,* var. ramonense, *261; oppositifolium, 245;* Ottonis, *264; pachycarpum, 261; paleaceum, 256; palmense, 278;* panamense, *292;* paniculatum, *293; paranthicum, 336;* Parkinsonianum, *264;* pendens, *294; peraltense, 262; pergameneum, 297;* physodes, *295; piliferum, 293; platycardium, 267; platychilum, 270;* platystigma, *295;* polyanthum, *297,* var. myodes, *298;* porpax, *298; porphyrophyllum, 298;* Powellii, *298;* prismatocarpum, *265;* probiflorum, *299; prorepens, 254; prostratum, 277;* pseudepidendrum, *299;* pudicum, *299; punctatum, 349; pusillum, 540;* pygmaeum, *265; quinquelobum, 297; radicans, 286,* var. *chiriquense, 286; Radlkoferianum, 269; ramonense, 261; ramonianum, 295;* ramosum, *301,* var. angustifolium, *301,* var. *imbricatum, 301; reflexum, 293;* repens, *301; resectum, 293;* rigidum, *303,* var. angustisegmentum, *303;* Rousseauae, *267; ruscifolium, 206;* Sanchoii, *304; Sancti-Ramoni, 336; santaclarense, 301;* Schlecterianum, *304;* Schumannianum, *305;* sculptum, *306; serruliferum, 278; sessile, 445; simulacrum, 283;* spondianum, *267;* Stamfordianum, *268;* Stangeanum, *268;* stenopetalum, *270;* strobiliferum, *306;* subnutans, *308; subpatens, 290; subulatum, 488; subviolascens, 278; tenuiflorum, 276; teres, 308; teretifolium, 308,* var. *Powellianum, 308; tessellatum, 259;* tetraceros, *309;* trachythece, *309;* triangulabium, *310; tribuloides, 208; turialvae, 293; umbellatum, 281; Umlaufii, 259; undulatum, 522; utricularioides, 478;* varicosum, *269; variegatum, 260; verecundum, 306; viscidum, 257;* volutum, *269;* Warszewiczii, *310*

Epithecia, 573; Morrisii, 574; panamensis, 576

Epithecium, 573

Eriopsis, *377;* rutidobulbon, *378*

Eriphilema, 36

Erythrodes, *160;* Killipii, *160*

Ethanium, 58

Eucharis, *23;* Bouchei, *24;* candida, *23*

Eucnemis, 352

Eulophia, *347;* alta, *347; longifolia, 347; Woodfordii, 347*

Eurystylus, 74; flaccida, 76

Euthonaea, 245; imbricata, 245; oppositifolia, 245

Eveltria, 41

Evelyna, 128; aurantiaca, 130; capitata, 129; hymenophora, 129

F

Fabricia, 18

Fernandezia, 552, 573; acuta, 553; robusta, 558

Fourcroea, 13

Fourcroya, 13; gigantea, 13; tuberosa, 13

Franquevillea, 18

Fregia, 133; amabilis, 136

Funium, 13

Furcraea, *13;* cabuya, *13,* var. integra, *13*

Furcroea, 13

G

Galathea, 34; coerulea, 35; speciosa, 35

Galeandra, *332; Batemanii, 332;* Baueri, *332;* juncea, *335*

Galeottia, 417; grandiflora, 417

Gethyra occidentalis, 59

Ghiesbreghtia, 337; calanthoides, 339; mexicana, 339

Ginger, *57*

Gladiolus, *34*

Glissanthe, 63

Glumosia, 36

Gomphichis, 145; costaricensis, 145

Gongora, *395;* armeniaca, *396,* var. bicornuta, *398; Boothiana, 398; bufonia, 401; fulva, 401; Jenischii, 398; leucochila, 398;* maculata, *398,* var. latibasis, *401,* var. tricolor, *401; negrita, 398;*

odoratissima, 398; Powellii, 398; quadricornis, 398; retrorsa, 398; Shepherdii, 398; superflua, 398; truncata var. *alba, 398; unicolor, 398; vitellina, 398*
Goodyera guyanensis, 153
Govenia, *352;* ciliilabia, *533;* liliacea, *353; Powellii, 353; utriculata, 353*
Gyas, 339
Gymnadenia, 117
Gymnosiphon, *44;* panamensis, *45;* suaveolens, *44*
Gynizodon, 513
Gyrostachys, 152; aguacatensis, 153; costaricensis, 154; picta, 156; Prasophyllum, 154

H

Habenaria, *117;* alata, *118;* avicula, *119;* bicornis, *120;* heptadactyla, *122;* monorrhiza, *119; patentiloba, 119;* pauciflora, *120;* petalodes, *119; petalodes* var. *micrantha, 119;* repens, *122; setifera, 120; spathacea, 120; Warszewiczii, 119*
Habranthus, 21
Haemodoraceae, *11*
Hedychium, *57;* coronarium, *57*
Helcia, 481
Heliconia, Beefsteak, *51*
Heliconia, *48; acuminata, 55; angusta, 55; aurantiaca, 56; aureo-striata, 51; austro-caledonica, 51; barqueta, 51;* Bihai, *51; Biahij, 51; Borinquena, 51; Bourgaeana, 51; buccinata, 51; cannoidea, 56; caribaea, 51; Champneiana, 51; Choconiana, 55; conferta, 50; curtispatha, 54; dasyantha, 53; densa, 50; elegans, 50; elongata, 51; hirsuta, 56,* var. *cannoidea, 56;* imbricata, *50; indica, 51;* Lankesteri, *52;* latispatha, *52; longa, 54; marantifolia, 56; marginata, 54;* Mariae, *50; meridensis, 52; nutans, 53; pendula, 54;* platystachys, *54; Poeppigiana, 51;* psittacorum, *56; punicea, 50; purpurea, 51; reticulata, 50;* rostrata, *54; rutila, 51; Seemannii, 51; straminea, 56;* subulata, *55; tortuosa, 53;* vellerigera, *54;* villosa, *53; Wagneriana, 50*
Heliconiopsis, 48; amboinensis, 51
Hellenia, 63
Helmia recemosa, 31
Hemp, Manila, *48*
Heterotaxis, 431; crassifolia, 445
Hexadesmia, 318; Acostaei, 320; fasciculata, 320; Lindeniana, 320; micrantha, 319; pachybulbon, 320; Powellii, 320
Hexisea, *245;* bidentata, *245; imbricata, 245; oppositifolia, 245*
Hippeastrum, *12*
Hoja blanca, *84*
Hormidium, 247; pseudopygmaeum, 265
Humboltia, 162
Huntleya, *427, 429; Burtii, 429; cerina, 427; marginata, 424; meleagris, 429*
Hydastylus, 36
Hymenocallis, 24; acutifolia, 25; americana, 25; disticha, 25; Dryandri, 25; littoralis, 25; Staplesiana, 25
Hymenocalyx, 24
Hypoxis, *18; caricifolia, 18;* decumbens, *18; decumbens* var. *mexicana, 18; gracilis, 18;* humilis, *18; scorzoneraefolia, 19*

I

Iantha, 476; pallidiflora, 478
Indian Shot, *75*
Inopsis, 476
Ionopsis, *476; pallidiflora, 478; paniculata, 478; tenera, 478;* utricularioides, *478; zonalis, 478*
Iridaceae, *34*
Ischnosiphon, *97;* leucophaeus, *98;* Morlaei, *101;* Pittieri, *101;* pruinosus, *99*
Isochilus, *329; chiriquensis, 329; linifolium, 132;* major, *329; prolifera, 321*
Ixia Xiphidium, 11

J

Jacuanga, 63
Jenmania, 143
Jimensia, 330
Jocaste, 5
Jonker, F. P., *42*
Juncaceae, *1*
Juncodes giganteum, 1
Juncus, *2*

K

Katubala, 74
Kefersteinia, 419; costaricensis, 422; lactea, 423
Kegelia, 379; Houtteana, 380
Kegeliella, *379;* Houtteana, *380;* Kupperi, *380*
Kerchovea, 103
Killip, E. P., *14*
Koellensteinia, *415;* Kellneriana, *416*
Kranzlinella, 191; platyrachis, 230

L

Laelia, *314;* Lueddemanii, *315; peduncularis, 314; rubescens, 314*
Languas, *57*

Leiochilus, 546; *retusus*, 548
Leochilus, 546; *cochlearis*, 547; labiatus, 547; *major*, 548; *Powellii*, 548; scriptus, 548
Lepanthes, 187; *abnormis*, 190; chiriquensis, 187; eciliata, 188; elata, 188; eximia, 190; insectiflora, 190; Maxonii, 188; *micrantha*, 187; rotundifolia, 189; turialvae, 189
Leucohyle, 481; *subulata*, 489; *Warscewiczii*, 488
Lichterveldia, 492
Licinia, 2
Liliaceae, 2
Limnorchis, 117
Limodorum altum, 347; *Lankesteri*, 342; *purpureum*, 340; *utriculatum*, 353; *verecundum*, 340
Lindleyella, 408; *picta*, 409
Lindsayella, 133; *amabilis*, 137
Liparis, 243; elata, 243; *eustachys*, 242; *fratrum*, 242; *labiata*, 547; *tipuloides*, 242; *Wendlandii*, 242
Liriamus, 19
Lirio, 20
Lobelia aphylla, 47
Lockhartia, 552; acuta, 553; amoena, 555, var. triangulabia, 556; *chiriquiensis*, 556; *costaricensis*, 555; elegans, 560; *grandibracteata*, 555; *lamellosa*, 558;*Lankesteri*, 556; micrantha, 556; mirabilis, 560; obtusata, 558; obtusifolia, 560; Oerstedii, 558; *pallida*, 553; Pittieri, 559; *robusta*, 558; *triangulabia*, 556; *variabilis*, 559; *verrucosa*, 558
Lophiaris, 514
Luddemania, 381
Lueddemannia, 381
Luedemannia, 381
Luzula, 1; gigantea, 1; *gigantea* var. *vulcanica*, 1; *latifolia*, 1; *paniculata*, 1
Lycaste, 410; *aciantha*, 449; *Bradeorum*, 415; brevispatha, 411; Campbellii, 411; *candida*, 411; *Dowiana*, 412; *Filomenoi*, 412; macrophylla, 412; *plana*, 412; Powellii, 413; tricolor, 415

M

Macradenia, 570; Brasavolae, 571
Macrochilus, 513
Macroclinium, 566
Malacarya, 104
Malaxis, 234; blephariglottis, 241; *brachyrrhyncha*, 240; *carpinterae*, 238; *caudata*, 506; *cochleariaefolia*, 235; excavata, 238; fastigiata, 240; *hastilabia*, 238; *ichthiorhynca*, 235; *Lankesteri*, 240; *macrostachya*, 236; majanthemifolia, 235; *montana*, 236; Parthonii, 240, var. denticulata, 241; Pittieri, 236; simillima, 238; Soulei, 236; tipuloides, 242; *uncinata*, 238; *Wendlandii*, 242; *Wercklei*, 241; Woodsonii, 239
Manila Hemp, 48
Maranta, 101; *Allouia*, 86; arundinacea, 101; *Cachibou*, 83; *Casupo*, 83; *clavata*, 89; *flexuosa*, 104; *geniculata*, 104; *indica*, 101; *Jacquinii*, 104; *lutea*, 83, 104; *micans*, 94; *protracta*, 101; *pruinosa*, 100; *silvatica*, 101; *Warscewiezii*, 92
Marantaceae, 81
Marantopsis, 103; *lutea*, 104
Marica, 34, 35; *caerulea*, 35; *gracilis*, 35; *micrantha*, 37; *paludosa*, 36; *tinctoria*, 40
Masdevallia, 179; Allenii, 185; *aperta*, 232; attenuata, 180; chontalensis, 182; collina, 180; *diantha*, 182; ecaudata, 182; *Lauchеana*, 180; Livingstoneana, 182; *panamensis*, 182; *platyrachis*, 230; simula, 185; tenuissima, 184
Mathieua, 23
Maxillaria, 431; *Abelei*, 464; *aciantha*, 449; *acutifolia*, 437; alba, 436; Allenii, 436; *Amparoana*, 463; *ampliflora*, 440; *angustifolia*, 467; angustisegmenta, 437; angustissima, 437; arachnitiflora, 438; *aurantiaca*, 468; Biolleyi, 439; *Boothii*, 256; brachybulbon, 439; Bradeorum, 440; *Brenesii*, 463; brevipes, 440; Camaridii, 442; chartacifolia, 443; *chiriquensis*, 467; *concava*, 407; conduplicata, 443; confusa, 444; *costaricensis*, 467; crassifolia, 445; ctenostachya, 446; *ctenostachys*, 446; cucullata, 446; dendrobioides, 447; diuturna, 448; *elongata*, 406; exaltata, 448; *foveata*, 407; Friedrichsthalii, 449; fulgens, 451; *gatunensis*, 445; *Henchmanni*, 467; inaudita, 451; *iridifolia*, 466; *lactea*, 463; *Lankesteri*, 468; *Lindeniana*, 446; longipetiolata, 452; luteo-alba, 454; *luteo-grandiflora*, 454; *Lyonii*, 467; *Macleei*, 465; *macrophylla*, 412; maleolens, 454; *meleagris*, 446; minor, 455; neglecta, 455; *obscura*, 446; oreocharis, 457; *panamensis*, 467; parvilabia, 458; Pittieri, 458; planicola, 460; Powellii, 461; *pubilabia*, 463; *puncto-striata*, 446; repens, 461; *revoluta*, 467; *rhodosticta*, 449; ringens, 463; *Rousseauae*, 463; rufescens, 464; *sessilis*, 445; *stachybiorum*, 407; *stenostele*, 465; *tricolor*, 415; *Turckheimii*, 463; *turialbae*, 449; umbratilis, 464; uncata, 465; vagans, 466; valenzuelana, 466; variabilis, 467; Wercklei, 468
Medora, 5

Meliclis, 402
Menadena, 431
Mesochloa, 21
Mesospinidium, 491; Warscewiczii, 491
Microstylis, 234; *blephariglottis*, 241; *brachyrrhynchos*, 240; *Brenesii*, 241; *cochlearifolia*, 235; *elegantula*, 235; *excavata*, 238; *fastigiata*, 240; *hastilabia*, 238; *histionantha*, 240; *ichthiorrhyncha*, 235; *majanthemifolia*, 235; *montana*, 236; *Parthonii*, 241, var. *denticulata*, 241; *Pittieri*, 236; *simillima*, 238; *tipuloides*, 242; *Wercklei*, 241
Miltonia, 513; Endresii, 513; Roezlii, 514; *superba*, 513
Monacanthus, 359
Monachanthus, 358
Monostiche, 82
Moorea, 386; *irrorata*, 386
Moraea, 34; *acorifolia*, 41; *chimboracensis*, 41; *gladioloides*, 41
Mormodes, 354; *atro-purpurea*, 356; atropurpureum, 355; *barbatum*, 356; colossus, 355; Hookeri, 356; igneum, 357; *macranthum*, 355; *Powellii*, 355; *Wendlandii*, 355
Morton, C. V., 6, 26
Musa, 48; *Bihai*, 51; Cavendishii, 48; Ensete, 48; paradisiaca, 48; sapientum, 48; textilis, 48
Musaseae, 48
Myanthus, 358
Myrosma, 95; dasycarpa, 96; *Guapilesense*, 104; Hoffmannii, 96; panamensis, 96

N

Name, 26
Nanodes, 247; *discolor*, 304
Nardo, 12
Neippergia, 381; *chrysantha*, 382
Nemepiodon, 24
Nemitis, 46
Neobartlettia, 143
Neolexis, 5
Neomarica, 34; caerulea, 35; gracilis, 35
Neomoorea, 386; irrorata, 386
Neottia acaulis, 156; *glandulosa*, 150; *orchioides*, 158; *picta*, 156; *speciosa*, 157
Nidema Boothii, 256, var. *triandrum*, 264; *ottonis*, 264
Niobea, 18; *pratensis*, 18
Notylia, 566; *angustilancea*, 567; Barkeri, 567; *Bernoulii*, 567; *bipartita*, 567; *Brenesii*, 567; Cordesii, 568; *gracilispica*, 569; *guatemalensis*, 567; *Huegelii*, 567; latilabia, 568; *multiflora*, 567; panamensis, 569; pentachne, 569; *Pittieri*, 567; *tamaulipensis*, 567; *tridachne*, 567; *trisepala*, 567; *turialbae*, 567

O

Oakes-Amesia, 564; cryptantha, 565
Obsitila, 2
Odontoglossum, 492; *Aspasia*, 501; caniniferum, 493; chiriquense, 494; convallarioides, 495; *coronarium*, 494; Egertoni, 495; *grande* var. *pallidum*, 498; *hastilabium*, 493; *Insleayi* var. *macranthum*, 498; Oerstedii, 496; *Powellii*, 498; Schlieperianum, 498; *Warscewiczii*, 498, 513
Oerstedella centradenia, 276; *centropetala*, 276
Olgasis, 514
Olsynium, 36
Oncidium, 514; advena, 546; *altissimum*, 519, var. β, 519, var. *Baueri*, 519; ampliatum, 517, var. majus, 519; ansiferum, 519; Baueri, 519; *Bernoullianum*, 517; *bifrons*, 545; bracteatum, 521; *Brenesii*, 533; *bryolophotum*, 530; Cabagrae, 521; *caesium*, 533; *cardiochilum*, 534; *caniniferum*, 493; carthaginense, 522; *carthaginense* var. *Oerstedii*, 522, var. *Swartzii*, 522; *caudatum*, 506; *cerebriferum*, 527; cheirophorum, 524; *chiriquense*, 494; *confusum*, 527; *convolvulaceum*, 528; *coronarium*, 494; crista-galli, 525; *decipiens*, 525; *Dielsianum*, 524; ebrachiatum, 527; ensatum, 527; *ensatum*, 519; *fulgens*, 533; *Geertianum*, 533; *Gireoudianum*, 510; globuliferum, 528; *globuliferum* var. *costaricense*, 528; *graciliforme*, 533; heteranthum, 530; *hieroglyphicum*, 519; *ionops*, 530; *iridifolium*, 525, 540; isthmi, 531; *Klotzschianum*, 533; Kramerianum, 532; *Kramerianum* var. *resplendens*, 532; *kymatoides*, 522; *labiatum*, 547; *lacerum*, 542; *Lankesteri*, 519; *megalous*, 530; *naranjense*, 519; nebulosum, 533; *nodosum*, 532; *obryzatoides*, 533; obryzatum, 533; *obsoletum*, 522; ochmatochilum, 534; *Oerstedii*, 522, var. *crispiflorum*, 522; onustum, 546; *palmophilum*, 349; panamense, 535; *panduriferum*, 522; panduriforme, 536; *Papilio* var. *Kramerianum*, 532; *papilioniforme*, 532; parviflorum, 536; *peliograma*, 546; *polycladium*, 519; Powellii, 538; pusillum, 540; *Rechingerianum*, 521; *scansor*, 528; *scriptum*, 548; stenotis, 541; stipitatum, 542; *stipitatum* var. *platyonyx*, 542; teres, 544; *undulatum*, 522; *varians*, 533; Warscewiczii, 545; *Wercklei*, 528
Onkeripus, 405, 431

Ophiomeris panamensis, *46*
Orchidaceae, *37*, *107*, *247*, *337*
Orchis monorrhiza, *119*
Oreolirion, *37*
Ornithidium, *431*; *album*, *442*; *anceps*, *455*; *Biolleyi*, *439*; *conduplicatum*, *443*; *fulgens*, *451*; *neglectum*, *455*; *Pittieri*, *458*; *Wercklei*, *468*
Ornithocephalus, *560*; bicornis, *561*; cochleariformis, *562*; *diceras*, *561*; *elephas*, *563*; inflexus, *563*; *lanuginosus*, *561*; *mexicanus*, *563*; *Pottsiae*, *563*; Powellii, *563*; *Tonduzii*, *563*; *xiphochilus*, *561*
Ornithophora, *548*
Orthrosanthus, *41*; chimboracensis, *41*
Osmoglossum, *492*; *acuminatum*, *495*; *anceps*, *495*; *convallarioides*, *495*; *Egertoni*, *495*

P

Palma, *12*
Palma del Norte, *12*
Palmita, *12*
Palmorchis, *143*; Powellii, *144*; trilobulata, *144*
Palumbina, *514*
Pancratio-Crinum, *19*
Pancratium, *24*; *americanum*, *25*; littorale, *25*
Paneguia, *36*
Panstrepis, *402*
Paphiopedilum, *114*; *caudatum*, *116*; *Hincksianum*, *117*; *longifolium*, *117*
Paphiopedium longifolium, *117*
Papiliopsis, *514*; *nodosus*, *532*
Pelexia, *152*; *congesta*, *160*; *Funckiana*, *158*; *guatemalensis*, *160*; *Pringlei*, *158*
Pentulops, *405*, *431*
Peperidium, *58*
Peristeria, *384*; elata, *384*; *Humboldtii*, *382*
Peristera, *384*
Peronia, *104*
Pescatorea, *426*, *427*; cerina, *427*
Phadrosanthus, *514*
Phaedrosanthus ciliaris, *257*
Phalanganthus, *2*
Phragmipedium, *114*; caudatum, *116*; longifolium, *116*
Phragmopedilum, *114*; *Warszewiczianum*, *116*
Phrynium altissinum, *94*; *cylindricum*, *87*; *floribundum*, *89*; *microcephalum*, *94*; *villosum*, *85*; *violaceum*, *89*; *Warscewiczii*, *92*
Phyllodes inocephalum, *94*
Physanthera, *478*
Physinga, *247*
Physosiphon, *176*; minutiflorus, *176*
Physurus, *160*
Pilumna, *481*
Pittierella, *472*
Planera, *63*
Plantain, *48*
Plantanillo, *48*, *75*
Plátano, *48*
Platanthera, *117*
Platyglottis, *327*; coriacea, *327*
Platystele, *191*
Plectronema, *21*
Pleiostachya, *97*; *Morlaei*, *101*; *Pittieri*, *101*; *pruinosa*, *100*
Pleurothallis, *191*; *acrisepala*, *210*; *Alexanderae*, *208*; Allenii, *205*; alpina, *212*; antonensis, *199*; *aperta*, *232*; arietina, *199*; aristata, *226*; barbae, *234*; *barboselloides*, *210*; *biflora*, *225*; Blaisdellii, *196*; *Bourgeaui*, *217*; *brevis*, *195*; Brighamii, *210*; Broadwayi, *194*, var. *tricarinata*, *194*; calyptrostele, *225*; *canae*, *229*; cardiochila, *197*; *cerea*, *206*; *chiriquensis*, *218*; cobraeformis, *203*; *coccinea*, *480*; Cogniauxiana, *217*; concaviflora, *202*; crenata, *232*; *cucullata*, *221*; *dichotoma*, *226*; *diuturna*, *231*; *divexa*, *226*; dolichopus, *230*; *dryadum*, *224*; *dubia*, *223*; ellipsophylla, *222*; eumecocaulon, *205*; *falcatiloba*, *220*; *fallax*, *208*; filamentosa, *232*; *Fuegii* var. *echinata*, *226*; fulgens, *211*; gelida, *218*; *geminiflora*, *225*; Ghiesbreghtiana, *220*; glandulosa, *212*; *glomerata*, *206*; gnomonifera, *105*; Grobyi, *224*; *hamata*, *232*; hispida, *200*; homolantha, *201*; *Hunteriana*, *232*; *integrilabia*, *224*; *lamprophylla*, *230*; *Lankesteri*, *223*; lepidota, *217*; *longissima*, *220*; *lyroglossa*, *229*; macrantha, *227*; *mandibularis*, *217*; *marginata*, *224*; *megachlamys*, *228*; muricata, *231*; *myriantha*, *223*; *nemorum*, *201*; *Niederleinii*, *229*; octomeriae, *206*; ovatilabia, *224*; *panamensis*, *224*; *pauciflora*, *227*; *peraltensis*, *196*; *peregrina*, *230*; *periodica*, *210*; perpusilla, *234*; Pfavii, *230*; phyllocardia, *234*; phyllocardioides, *234*; *picta*, *224*; *Pittieri*, *218*; *platyrachis*, *230*; *poasensis*, *230*; *polystachya*, *217*; Powellii, *228*; praegrandis, *222*; pruinosa, *227*; pterocaulis, *214*; pyrosodes, *234*; *racemiflora*, *229*; rhodoglossa, *198*; rotundata, *196*; Rowleei, *221*; ruscifolia, *206*; segoviensis, *229*; simulans, *201*; *sororoa*, *231*; spectabilis, *231*; stenostachya, *223*, var. *Lankesteri*, *223*; subserrata, *233*; trachychlamys, *205*; triangulabia, *198*; tribuloides,

208; Tuerckheimii, *228*; uncinata, *208*; *valenzuelana*, *466*; velaticaulis, *218*; verecunda, *214*; *vittariifolia*, *212*; vittata, *217*; *Wagneri*, *229*; *Williamsii*, *194*; xanthophthalma, *233*;
Pogadelphia, *36*
Pogonema, *21*
Pogonia, *123*; cubensis, *125*; mexicana, *125*; rosea, *123*; *Wagneri*, *125*
Polianthes, *12*
Polycycnis, *387*; barbata, *389*; *gratiosa*, *389*
Polygonastrum, *5*
Polystachya, *331*; cerea, *331*; *costaricensis*, *331*; Masayensis, *332*; *minor*, *331*; *panamensis*, *331*; *Powellii*, *331*
Ponera albida, *322*; *amethystina*, *322*; *Behrii*, *322*; *bilineata*, *325*; *mescopsis*, *323*
Ponthieva, *148*; *Brenesii*, *152*; *costaricensis*, *150*; Ephippium, *150*; *glandulosa*, *150*; *guatemalensis*, *150*; maculata, *152*; *oblongifolia*, *150*; racemosa, *150*; *rostrata*, *150*
Prescottia, *146*; oligantha, *146*; *panamensis*, *146*; stachyodes, *147*
Pseudepidendrum spectabile, *299*
Pseuderiopsis, *377*
Psittacoglossum, *431*
Psychopsis, *514*
Ptychomeria, *44*; *suaveolens*, *44*
Pyrolirion, *21*
Pyxa, *63*

R

Ravenala madagascarensis, *48*
Regnellia, *339*
Renealmia, *58*; aromatica, *59*; Arundinaria, *61*; cernua, *58*; chiriquina, *62*; concinna, *60*; costaricensis, *61*; *densiflora*, *61*; exaltata, *62*; mexicana, *60*; *occidentalis*, *59*; rubro-flava, *62*; *strobilifera*, *58*
Restrepia, *191*; *filamentosa*, *232*; *Lansbergii*, *233*; *Powellii*, *233*; *subserrata*, *233*; *Tonduzii*, *233*; *xanthophthalma*, *233*
Rhynchadenia, *570*
Rhynchostele, *546*
Rhynchostelis, *546*
Rodriguezia, *478*; *cochlearis*, *547*; compacta, *479*; *lanceolata*, *480*; secunda, *480*; *secunda* var. *panamensis*, *480*
Rodwaya, *45*
Rolfea, *143*; *Powellii*, *144*

S

Sagú, *81*, *103*
Sansevieria, *2*
Saranthe, *95*
Sarcoglottis, *152*; *Hunteriana*, *156*; *picta*, *156*; *Powellii*, *156*; *Purpusiorum*, *156*
Satyrium orchioides, *158*; *plantagineum*, *157*
Scadianus, *19*
Scaphosepalum, *186*; elasmotopus, *186*; *longirepens*, *186*; *panamense*, *182*
Scaphyglottis, *318*; Acostaei, *320*; *albida*, *322*; amethystina, *322*; Behrii, *322*; bilineata, *325*; *brachiata*, *322*; cuneata, *320*; dolichophylla, *327*; *gracilis*, *321*; laevilabia, *321*; Lindeniana, *320*; longicaulis, *321*; mesocopsis, *323*; micrantha, *319* minutiflora, *323*; *pauciflora*, *322*; *Powellii*, *323*; *prolifera*, *320*; tenella, *325*; *unguiculata*, *321*; *Wercklei*, *321*
Schomburgkia, *314*; *Lueddemanii*, *315*
Schweinfurth, Charles, *337*
Selenipedium, *114*; chica, *114*; *longifolium*, *117*
Serapias speciosa, *157*; *flava*, *161*
Serrastylis, *570*
Sievekingia, *378*; suavis, *378*
Sigillaria, *5*
Sigmatostalix, *548*; abortiva, *549*; *costaricensis*, *551*; guatemalensis, *551*; hymenantha, *551*; *poikilostalix*, *551*; racemifera, *552*
Siphotoma, *24*
Sisyrinchium, *36*; *alatum*, *38*; arizonicum, *40*; chiricanum, *40*; convolutum, *38*; *iridifolium*, *38*; Mandoni, *39*; *micranthenum*, *37*; micranthum, *37*; *Moritzianum*, *41*; *rigidum*, *40*; tinctorium, *40*; *tingens*, *40*
Smilacaceae, *6*
Smilacina, *5*; *laxiflora*, *5*; *nervulosa*, *5*; paniculata, *5*; *thyrsoidea*, *5*; *Gigas*, *6*
Smilax, *6*; *calocardia*, *10*; chiriquensis, *9*; domingensis, *8*; *Houstoniana*, *7*; lappacea var. ornata, *8*; *mexicana*, *7*; mollis, *10*; panamensis, *9*; *ramonensis*, *9*; *Schlechtendalii*, *8*; spinosa, *7*, var. compta, *8*; spissa, *8*; subpubescens, *10*; *Wagneriana*, *7*
Sobralia, *133*; Allenii, *134*; amabilis, *136*; Bletiae, *136*; Bouchei, *136*; callosa, *137*; decora var. aerata, *140*; *epiphytica*, *142*; *eublepharis*, *137*; Fenzliana, *137*; fragrans, *137*; labiata, *138*; leucoxantha, *138*; Lindleyana, *138*; macrophylla, *143*; panamensis, *140*; *panamensis* var. *albiflos*, *140*; *Powellii*, *138*; Rolfeana, *140*; suaveolens, *142*; valida, *142*; Warscewiczii, *143*
Solenidium Endresii, *491*
Solenipedium, *114*
Souza, *36*
Spathiger, *247*; *rigidus*, *303*; *strobiliferus*, *306*

Spathirachis, *37*
Spider lily, *25*
Spiranthes, *152*; acaulis, *156*; *aguacatensis*, *153*; *colorata*, *157*; costaricensis, *154*; *epiphytica*, *154*; *Funckiana*, *158*; guyanensis, *153*; *jaliscana*, *158*; navarrensis, *157*; orchioides, *158*; Prasophyllum, *154*; speciosa, *157*; *subpandurata*, *154*; Woodsonii, *155*
Spirostalis, *104*
Sprekelia, *12*
Stanhopea, *389*; *amoena*, *394*; *aurea*, *394*; *bucephalus*, *391*; *costaricensis*, *390*; graveolens, *390*; *inodora*, *390*; oculata, *391*, var. *constricta*, *390*; pulla, *392*; *venusta*, *394*; Wardii, *394*; *Warscewicziana*, *390*
Stanhopeastrum, *389*
Stelis, *161*; aemula, *174*; Allenii, *164*; atrorubens, *166*; *barbata*, *165*; *bryophila*, *165*; *cascajalensis*, *169*; *chiriquensis*, *165*; *cinerea*, *165*; collina, *175*; *costaricensis*, *165*; crescentiicola, *169*; *cuspidilabia*, *169*; despectans, *165*; Endresii, *171*; *eximia*, *169*; *flexuosa*, *169*; hymenantha, *169*; inaequalis, *164*; *Isthmii*, *169*; leucopogon, *169*; longipetiolata, *175*; Maxonii, *173*; microchila, *165*; montana, *166*; *nutantiflora*, *165*; panamensis, *173*; *parvibractcata*, *171*; Powellii, *172*; *praemorsa*, *169*; *sarcodantha*, *174*; *seleniglossa*, *160*; Skutchii, *167*; Storkii, *172*; vestita, *174*; Williamsii, *175*
Stellarioides, *2*
Stemoptera, *46*
Stenocoryne, *408*
Stenoptera, *145*; *costaricensis*, *145*
Stenorrhynchus, *152*; *jaliscana*, *158*; *navarrensis*, *157*; *orchioides*, *158*; *speciosus*, *157*
Stromanthe, *103*; lutea, *104*
Styrandra, *5*

T

Taetsia, *2*
Tanghekolli, *19*
Telipogon, *571*; dendriticus, *572*; radiatus, *572*
Telopogon, *571*
Tetragamestus gracilis, *320*
Thalia, *104*; *altissima*, *105*; *angustifolia*, *105*; *erecta*, *104*; geniculata, *104*
Thelypogon, *571*
Thiebautia, *339*
Thismia, *45*; panamensis, *46*
Thorvaldsenia, *343*
Tigridia, *34*
Todaroa, *578*
Tolumnia, *514*
Tomodon, *24*
Tovaria, *5*; *laxiflora*, *5*; *nervulosa*, *5*; *thyrsoidea*, *5*
Trachinema, *2*
Traveler's Tree, *48*
Tribrachys, *45*
Trichocentrum, *475*; panamense, *476*
Trichophila, *481*
Trichopilia, *481*; *coccinea*, *486*; *crispa*, *486*; *hymenantha*, *489*; *jamaicensis*, *489*; *Kienastiana*, *488*; *lepida*, *486*; leucoxantha, *482*; maculata, *484*; marginata, *486*, var. *alba*, *486*, var. *lepida*, *486*, var. *olivacea*, *488*; *Powellii*, *484*; suavis, *488*; subulata, *488*; turialbae, *490*
Tridachne, *566*; *virens*, *567*
Trigonidium, *469*; Egertonianum, *469*; Lankesteri, *471*; obtusum, *471*; *Seemanni*, *469*
Triphora, *123*; *cubensis*, *125*; *mexicana*, *125*; *Wagneri*, *125*
Tripterella, *43*; *capitata*, *43*
Tritonia, *34*
Trixeuxis, *480*
Trizeuxis, *480*; *andina*, *481*; falcata, *481*
Trophianthus, *499*
Tsiana, *63*
Tuberose, *12*
Tylochilus, *349*

V

Vagnera, *5*
Vanilla, *126*; *fragrans*, *126*; *Pittieri*, *128*; planifolia, *126*; pompona, *128*
Vellosia, *25*
Vellozia, *25*; panamensis, *26*
Velloziaceae, *25*
Vellozoa, *25*
Vogelia, *43*; *capitata*, *43*

W

Waluewa, *546*
Warczewiczella, *419*
Warrea, *351*; costaricensis, *352*; *discolor*, *423*; *graveolens*, *416*; *marginata*, *424*; *quadrata*, *424*
Warscewiczella, *419*; *aromatica*, *421*; *caloglossa*, *421*; *discolor*, *423*; *Wendlandii*, *421*; *velata*, *424*
Warszewiczella, *419*; *marginata*, *424*
Warscewitzia, *359*
Wild banana, *48*
Wild plantain, *48*
Williams, Louis O., *107*, *247*, *337*

X

Xaritonia, *514*
Xeilyathum, *514*
Xiphidium, *11*; *album*, *11*; caeruleum, *11*; *floribundum*, *11*; *giganteum*, *11*
Xylobium, *405*; *concavum*, *407*; elongatum, *406*; *Filomenoi*, *407*; foveatum, *407*; Powellii, *407*; *stachybiorum*, *407*; *sublobatum*, *407*
Xyphostylis, *74*

Y

Yam, *26*

Z

Zelmira, *82*
Zephyranthes, *21*; citrina, *21*; *Eggersiana*, *22*; *Lindleyana*, *22*; *Mesochloa*, *22*; *nervosa*, *22*; rosea, *22*; tubispatha, *22*
Zingiber, *57*
Zingiberaceae, *57*
Zygopetalon, *417*
Zygopetalum, *417*, *427*; *aromaticum*, *421*; *Burtii*, *429*; *cerinum*, *427*; *discolor*, *423*; grandiflorum, *417*; *lacteum*, *423*; *meleagris*, *429*; parviflorum, *419*; *quadratum*, *424*; *Wendlandii*, *421*
Zygostates costaricensis, *561*

STAFF
OF THE MISSOURI BOTANICAL GARDEN

Director
GEORGE T. MOORE

HERMANN VON SCHRENK,
Pathologist

JESSE M. GREENMAN,
Curator Emeritus of the Herbarium

CARROLL W. DODGE,
Mycologist

EDGAR ANDERSON,
Geneticist

ROBERT E. WOODSON, JR.
Curator of the Herbarium

HENRY N. ANDREWS,
Paleobotanist

ROBERT W. SCHERY,
Research Associate

GUSTAV A. L. MEHLQUIST,
Research Horticulturist

ROLLA M. TRYON,
Assistant Curator of the Herbarium

GEORGE B. VAN SCHAACK,
Honorary Curator of Grasses

JULIAN A. STEYERMARK,
Honorary Research Associate

NELL C. HORNER,
Librarian and Editor of Publications

GERALD ULRICI,
Business Manager

BOARD OF TRUSTEES
OF THE MISSOURI BOTANICAL GARDEN

President
RICHARD J. LOCKWOOD

Vice-President
DANIEL K. CATLIN

Second Vice-President
EUGENE PETTUS

L. RAY CARTER
DUDLEY FRENCH
HENRY HITCHCOCK
JOHN S. LEHMANN
GEORGE T. MOORE
A. WESSEL SHAPLEIGH
ETHAN A. H. SHEPLEY

EX-OFFICIO MEMBERS

ARTHUR H. COMPTON,
Chancellor of Washington University

JOSEPH M. DARST,
Mayor of the City of St. Louis

WILLIAM P. GRUNER,
President of the Academy of Science of St. Louis

WILLIAM SCARLETT,
Bishop of the Diocese of Missouri

WILLIAM SCHUMACHER
President of the Board of Education of St. Louis

GERALD ULRICI, *Secretary*

Volume XXXVI Number 3

Annals of the Missouri Botanical Garden

SEPTEMBER, 1949

Evidence, excluding Mutations, Polysomy, and Polyploidy, as Possible Causes of Non-Mendelian Segregations in *Saccharomyces* . . . . . Balaji D. Mundkur 259–280

New Species of *Lonchocarpus* from Panama . . . . . Frederick J. Hermann 281–284

A First Record for the Genus *Qualea* (Vochysiaceae) from North America (Panama) . . . . . Robert W. Schery 285–286

Some Pteridosperm Stems and Fructifications with Particular Reference to the Medullosae . . . . . Robert W. Baxter 287–352

Maize Among the Hill Peoples of Assam . . . . . C. R. Stonor and Edgar Anderson 355–404

PUBLISHED QUARTERLY AT GALESBURG, ILLINOIS,
BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN,
ST. LOUIS, MISSOURI.

Entered as second-class matter at the post-office at Galesburg, Illinois,
under the Act of March 3, 1879.

Annals
of the
Missouri Botanical Garden

A Quarterly Journal containing Scientific Contributions from the Missouri Botanical Garden and the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

Information

The ANNALS OF THE MISSOURI BOTANICAL GARDEN appears four times during the calendar year: February, May, September, and November. Four numbers constitute a volume.

Subscription Price ..... $10.00 per volume
Single Numbers ..... 2.50 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

Annals
of the
Missouri Botanical Garden

Vol. 36 SEPTEMBER, 1949 No. 3

EVIDENCE EXCLUDING MUTATIONS, POLYSOMY, AND POLYPLOIDY AS POSSIBLE CAUSES OF NON-MENDELIAN SEGREGATIONS IN SACCHAROMYCES[1]

BALAJI D. MUNDKUR[2]

Tetrad analysis, the direct genetical characterization of the segregation products of meiosis, has frequently revealed the occurrence of ratios differing from the 1:1 gametic segregations implicit in the postulates of classical Mendelian genetics. Although many of these exceptions to regular segregation have been reported in the fungi, which offer advantages for genetical analysis denied to the geneticist studying higher organisms, the bases for inferring such divergent segregations were not beyond criticism. Previous workers using the fungi as genetic material investigated inadequately marked stocks (generally only one marker was used) and the deduction of truly non-Mendelian ratios was therefore rendered ambiguous by the possible occurrences of chromosomal aberrations. The few markers used were not sufficient to establish hybridity of the stocks analyzed, and, usually being morphological, introduced obvious difficulties in diagnosing the segregants with accuracy. The occurrence of mutations in the segregants during vegetative growth prior to diagnosis was not excluded as a possible cause obscuring an initially Mendelian segregation.

The experiments reported in this paper were designed with the above considerations in view and present data eliminating the questionable features involved in evaluating non-Mendelian inheritance. In the tetrad analyses of the five hybrids

[1] An investigation carried out in the Henry Shaw School of Botany of Washington University, St. Louis, Mo., and Southern Illinois University, Carbondale, and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Henry Shaw School of Botany. This work was supported by grants from Anheuser-Busch, Inc., and the U. S. Public Health Service.

[2] Department of Microbiology, Southern Illinois University, Carbondale, Illinois.

discussed on the following pages, use has been made of a sufficient number of marker genes to enable inclusion of only legitimate matings in the data. Being biochemical, these markers in addition permit precise diagnosis of the segregants. The analyses, furthermore, have eliminated the possibilities of polysomy and polyploidy as mechanisms causing irregular segregations and have provided evidence that the latter may originate in the heterozygote as a result of gene conversions.

TETRAD ANALYSIS OF YEAST HYBRIDS

Lindegren and Lindegren (1946) analyzed extensive pedigrees of *Saccharomyces* hybrids for the inheritance of abilities to ferment galactose and melibiose. They discovered that, in some pedigrees, the capacity of haplophase clones to ferment each of these sugars was controlled by single genes *G* or *ME*, respectively. Haplophase clones bearing the recessive alleles *(g* and *me)* were incapable of fermenting galactose and melibiose; that is, they were incapable of producing detectable gas under the conditions of the Durham tube fermentation test. In asci heterozygous for *G/g* and *ME/me*, these alleles segregated in a Mendelian manner yielding two fermenter and two non-fermenter haplophase clones from each ascus. In other words, hybrid asci in these pedigrees were of the constitution *G G g g* (or *ME ME me me*).

In other pedigrees, tetrad analysis of hybrids heterozygous for abilities to ferment these sugars revealed occasional high frequencies of non-Mendelian segregations. In such exceptional tetrads, three or four of the single ascospore cultures exhibited the fermenter phenotype instead of the expected ratio of 2 fermenter : 2 non-fermenter clones; that is, some asci in these pedigrees segregated *G G G g* and *G G G G* (or *ME ME ME me* and *ME ME ME ME*) phenotypes.

Non-Mendelian irregularities in segregations of this nature were ascribed (Lindegren and Lindegren, 1946) to gene-initiated cytogenes. A non-uniform distribution of the cytogenes between homologous alleles was supposed to have occurred preceding spore formation, resulting in the transformation of recessive to apparently dominant alleles.

Further analyses of irregular segregations were made in a recent book (Lindegren, 1949) in which the Cytogene Theory was modified by assuming that cytogenes (called gene-products to prevent confusing them with plasmagenes) were solely gene-produced and were incapable of self-duplication. The multiple-factor hypothesis was shown to be inadequate for the explanation of the non-Mendelian segregations encountered.

The Plasmagene Theory elaborated by Spiegelman (1946) is an alternative view of the mechanism of non-Mendelian segregations in *Saccharomyces*. According to this theory, plasmagenes are autonomous (self-perpetuating) cytoplasmic entities capable of producing enzymes, and an unequal distribution of these entities in the cytoplasm at the time of spore formation is held to account for irregular ratios of fermenter : non-fermenter phenotypes. Arguments against the Plasma-

gene Theory have been considered in detail by Monod (1947) and Lindegren (1949).

Irregular segregations in heterozygotes with well-marked chromosomes have excluded the view that cytoplasmic components are involved in irregularly segregating tetrads. On the basis of these data, Lindegren (1949a) has proposed a gene-to-gene transfer of gene components in the heterozygote, and has embodied this concept in the Conversion Theory. This concept envisages the gene as a loosely organized, labile complex capable of sharing part of its essential components with its allele, thus endowing the allele with new or increased capacities. In parting with some of its essential constituents a gene, according to this view, is susceptible to partial degradation, and the deprivation, if excessive, may result in a weakening or even loss of the original capacities of the gene donating the constituents. The occurrence of tetrads with more than the expected number of fermenter segregants is explicable on the basis that recessives have been transformed to dominants in the heterozygote.

Experiments have adequately shown that the transformed recessive allele is capable of perpetuating the new capacity (acquired from the dominant gene) through successive generations. The acquisition of the capacities of the dominant gene by the recessive allele and the ability of this new character to segregate after crossing is, indeed, equivalent to mutation. The term "conversion" has been used, however, to denote a mutation occurring in and dependent on the heterozygous condition.

Mundkur and Lindegren (1949) demonstrated that the phenomenon of long-term adaptation to galactose could be explained as the result of the mutation of non-fermenter clones *(g)* to the fermenter allele *(G)*. The capacity for mutation was shown to be characteristic of certain lines in which it occurred with unusually high frequency. This raised the question whether the non-Mendelian segregations of galactose and melibiose phenotypes encountered in previous pedigrees were indeed instances of conversion in the heterozygote during meiosis, i.e., true conversions, or merely mutations occurring after the spore had germinated. However, the fact that the extra-fermenters in non-Mendelian tetrads ferment as rapidly as *bona fide* fermenter segregants makes this phenomenon different from that encountered in "slow"-fermenter pedigrees. In the latter case, the variable number of days elapsing before a "slow" clone ferments is indicative of chance mutation; however, an irregular tetrad is diagnosed as such only if more than the expected number of segregants ferment *at the same time*, usually within 18 hours; or if more than the expected number of segregants fail to ferment over an extended period of time.

Tetrad analysis involves the transfer of single-spore, glucose-grown micro-colonies to glucose agar slants. When the four haplophase clones have attained mature growth on the slants they are tested for their mating-type specificity and their abilities to ferment various sugars and synthesize vitamins, amino acids, and nucleic acid components. This initial growth on glucose may not involve selection

of phenotypes, and mutants of non-fermenter haplophase segregants *(g* or *me)* to fermenter phenotypes *(G* or *ME)* produced in genetically unstable lines should have equal opportunities for growth. When a hybrid ascus heterozygous for *G/g* and *ME/me* is dissected, one expects two ascospores to be non-fermenters. However, if mutation occurred on glucose after these two spores germinated, each segregant culture would comprise mixtures of original *g* and mutant *G* clones. When this mixed population is used as inoculum in testing for galactose (or melibiose) fermentation the mutant cells would be selected and would achieve fermentation. A highly mutable *(g* to *G; me* to *ME)* haplophase segregant is thus apt to be diagnosed as an extra-fermenter although the ascospore giving rise to the mutant clones was genotypically *g* or *me* when isolated from the ascus.

Similarly, loss mutations *(G* to *g; ME* to *me)* are apt to yield fewer than the expected number (two) of fermenter phenotypes when mature glucose-grown clones are tested for fermentation.

Situations such as these could obscure Mendelian segregations and lead to the incorrect conclusion that gene transformation had occurred. Originally *G G g g* spore tetrads (where either allele is highly mutable) might be finally diagnosed as *G G G G, G G G g, G g g g,* or *g g g g.*

A helpful criterion for determining whether the non-Mendelian segregations are cases of gene conversions or of mutations during growth on glucose would be, of course, the abilities of the four segregants to ferment at the earliest stage of growth, viz., the spore stage. In the absence of a test sufficiently sensitive to detect fermentation by a single spore, other means must be employed. The experiments reported herein were designed to test the fermentative abilities of tetrads derived from "converting" pedigrees under conditions in which their multiplication was restricted and therefore before their chances of mutation had obscured the results.

Previous pedigrees in which irregular segregations of galactose and melibiose markers were analyzed (Lindegren and Lindegren, 1946, table 2) were derived from crosses in which culture C1A was used as one of the parents. It is a single-spore culture derived from S. *carlsbergensis* (culture 126, Dr. Mrak) and its use as a parent causes marked disturbances in segregations in the progeny. It is an *α* mating type capable of fermenting sucrose, galactose, melibiose, alpha methyl glucoside and maltose; C1A is an adenine-independent white culture and is thiamin-, inositol-, and pantothenate-independent but is pyridoxine-dependent. The asci descended from C1A analyzed by Lindegren and Lindegren were characterized for only mating type specificity and galactose and melibiose fermentations. Moreover, these asci were produced by inducing mass copulations of haploid parents and the limited number of marker genes made their truly hybrid nature a debatable question.

In the present investigation, a sufficient number of marker genes was used to establish hybridity beyond any question. The use of the adenine-dependent, pink

haplophase cultures as mates for C1A and its close descendants afforded an added advantage. The pink cultures were descendants of a white clone treated with nitrogen mustard gas by Dr. E. L. Tatum and Mr. S. E. Reaume.

EVIDENCE THAT CONVERSIONS OF FERMENTER GENOTYPES ORIGINATE IN THE HETEROZYGOTE

Materials and methods: Five different crosses involving C1A and three of its direct descendants (607, 608, and 609) were made:—C1A × 3349; 609 × 3190; 607 × 3168; C1A × 5859; and 608 × M317. The spores were isolated on natural medium with glucose as a carbon source. Only 34 four- and three-spored viable asci from a total of 87 dissected have been included in the present analyses.

After all the four (or three) spores in a tetrad had germinated to produce microcolonies ranging in population from 100,000 to 500,000 cells per colony, each entire microcolony was transplanted and streaked over a small area on a glucose agar slant. This procedure insures a thorough mixing of mutant fermenter sectors that might have arisen during growth of the microcolony. A small number of cells was then immediately scraped off the slant surface and inoculated into molten 1.75 per cent nutrient agar at 40° C. containing 2 per cent galactose as the carbon source. This molten agar was poured over a layer of solidified non-nutrient 3 per cent agar in a sterile Petri plate. A third layer of non-nutrient agar was poured over the galactose agar after the latter had solidified. This method prevents the fermenter colonies in close proximity from being confluent in growth and also minimizes contaminations. The same procedure was employed in making melibiose pour-plates. Fig. 1 describes the method diagramatically.

The residual haplophase yeast on the slant was allowed to incubate 24 hours and was then streaked over the entire slant surface to obtain luxuriant growth. This tube was retained as the stock culture. Mature inoculum from the glucose slant was subsequently tested for mating type specificity and fermentative and vitamin-synthesizing abilities. Simultaneous tests for galactose and melibiose fermentation by colonies developing on galactose and melibiose pour-plates were conducted.

The data are presented in tables I–V. The capitals *G*, *ME*, *MG*, *S*, and *MA* indicate phenotypes fermenting galactose, melibiose, alpha methyl glucoside, sucrose, and maltose, respectively; the corresponding small letters denote the recessive, non-fermenter alleles. The number of days elapsing before a "slow" clone ferments is indicated by subscript numerals. White cultures are indicated by W and pink ones by P. Adenine-independence is denoted by *AD* while dependence is shown by *ad*. The alleles *TH/th*, *PN/pn*, *IN/in*, *PY/py* indicate abilities (or inabilities) to synthesize thiamin, pantothenate, inositol and pyridoxine, respectively.

EXPERIMENTAL RESULTS

The widespread disturbances in segregations of fermenter phenotypes (shown in tables I–V) are noteworthy, since the stocks to which C1A, 607, 608 and 609 were mated had been carefully selected for regular segregations for the characters.

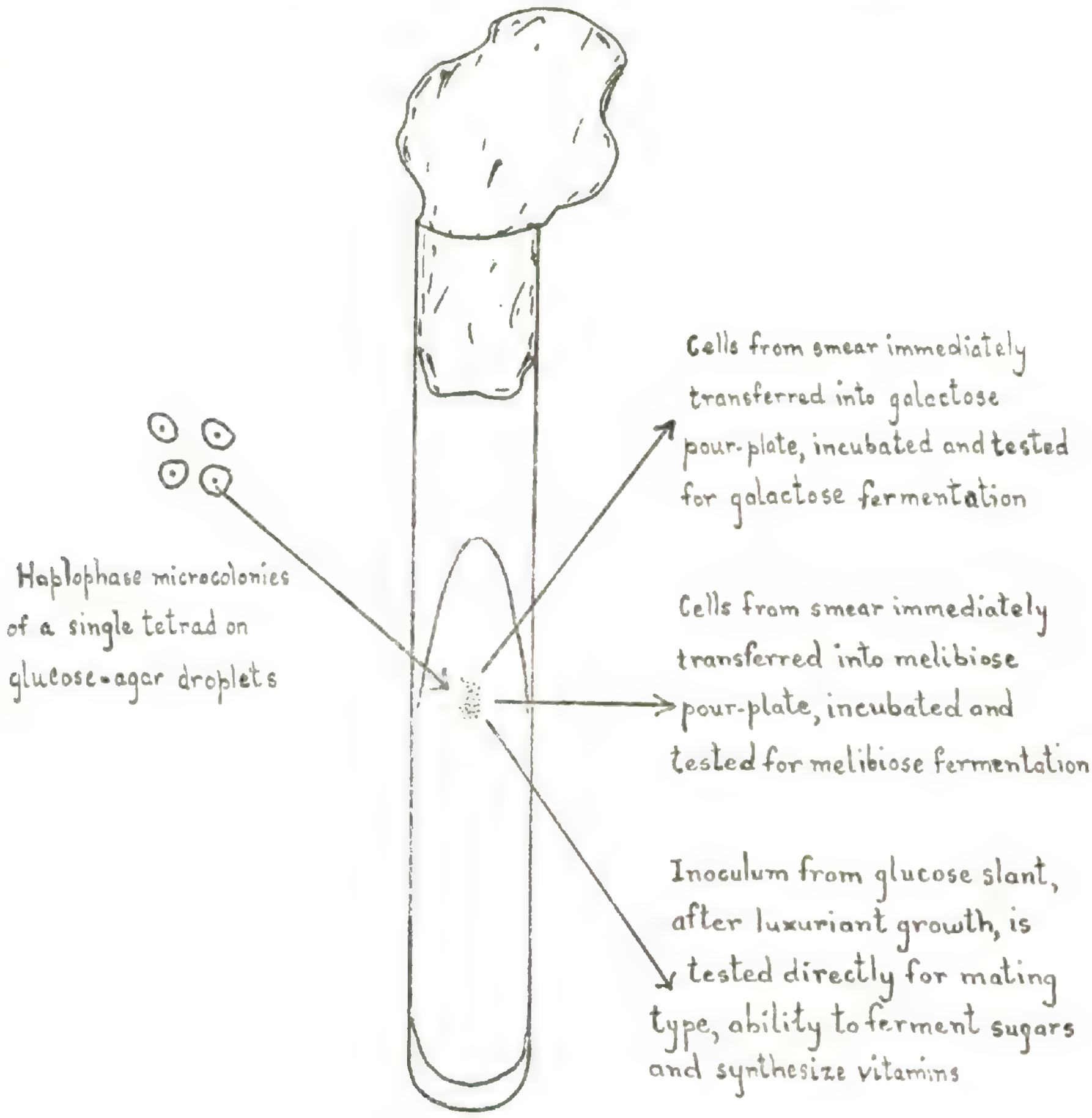


Fig. 1. Diagram showing the procedure adopted to minimize mutations in single spore clones and correlate fermentative capacities during two growth periods of a haplophase segregant.

In spite of the extensive non-Mendelian ratios, the truly hybrid nature of the asci analyzed is evident from the regular segregations of at least two marker genes in each ascus. Further support derives from the fact that cultures of C1A, 607, 608, and 609, and their mates are unable to copulate illegitimately and produce ascospores.

The possibility that a high rate of mutation of the non-fermenter recessive genes to dominance or of the fermenter gene to recessiveness would explain the irregularities in segregation was excluded by the fact that the haploid clones to which C1A, 607, 608, and 609 were mated had been derived from pedigrees in which the stability of the genotypes was pronounced. Further confirmation of the stability of the recessive parents was obtained by the procedure for detecting fermentation mutants described previously (Mundkur and Lindegren, 1949). No reversions to melibiose fermentations were detected in fifteen melibiose pour-plates

made with heavy inocula of glucose-grown, melibiose non-fermenter clones; the rates of reversion of galactose recessives were very low.

SEGREGATIONS OF GALACTOSE AND MELIBIOSE FERMENTER PHENOTYPES

It has been pointed out above that the ambiguity in deciding whether the extra-fermenters in *G G G g* and *G G G G* (or *ME ME ME me* and *ME ME ME ME*) tetrads originate from gene transformations or from mutations can be resolved by minimizing the chances of mutations in a haplophase segregant. The galactose and melibiose pour-plates made with inoculum obtained directly from the microcolonies provided data on this point. Since the mutation rates observed are usually of the order of 1×10^{-7} and the number of cells in a microcolony at the time of pouring plates does not exceed 500,000, the probability of recovering fermenter mutants may be assumed to be rather remote at this stage of growth. This assumption is strengthened, moreover, by the demonstration (cf. above) of the stability of the genotypes in the recessive parents.

The colonies in pour-plates of both galactose and melibiose agar are principally of three sizes on the fourth or fifth day after plating. These have been arbitrarily designated as large, medium, and minute colonies. The large colonies range in diameter from approximately 0.8 to 6 mm., while the medium-sized colonies are approximately 0.2 to 0.5 mm. in diameter. The minute colonies are visible as specks in the agar.

When a haploid clone is plated out, it may develop into uniformly sized colonies falling in any one of these categories, or a combination of two of these size classes; or it may show no growth at all. In tables I–V when one class alone is indicated for a segregant, it is implied that the colonies in that particular pour-plate are of uniform size. Plate 1 shows melibiose pour-plates of tetrad M532–M535, exemplifying these size classes.

The medium- and large-sized colonies are obviously fermenters and consistently corroborate the phenotype of the segregant obtained from the corresponding glucose slant. However, the minute colonies may or may not be fermenters. For instance, on plates where both minute and large colonies occur, single minute colonies inoculated with a micropipette into sugar broth achieve fermentation and confirm the characteristic of the clone from the corresponding slant. In other cases, however, minute colonies occurring uniformly in a plate were generally non-fermenters.

Evidence that the differences in colony sizes in a fermenter clone result not from differences in fermentative ability but really from differing growth rates was obtained from the following experiment: A suspension of a single minute fermenter colony (clone M533) from a galactose plate was plated out in galactose agar and was found to yield only minute colonies. A galactose pour-plate of a suspension of a single large fermenter colony of the same clone produced both large and minute colonies. Therefore, the minute colonies are slower-growing clones descended from the large-colonied clones. This explains the occurrence of

TABLE I

TETRAD ANALYSIS OF CONVERTER BY STANDARD HYBRID ASCI, *C1A* BEING THE CONVERTER

(*C1A a G ME MG MA AD*(W) *TH PN IN py* × 3349 a *g me mg ma ad*(P) *TH pn in py*)

Tetrad phenotypes	Size of colonies in pour-plates		Fermentation by inocula from pour-plates	
Inocula derived from glucose slants	Gal. plates	Mel. plates	Gal. plates to gal. broth	Mel. plates to mel. broth
M528 a *G ME MG MA AD* (W) *pn in*	med.	lge.	+	+
M529 a *G ME MG MA AD* (W) *pn IN*	med.	min.	+	+
M530 a *G ME MG MA AD* (W) *PN IN*	med.	min.	+	+
M531 a *G ME MG MA AD* (W) *PN in*	med.	lge.	+	+
M532 a *G ME MG MA ad* (W) *pn in*	lge.	lge.	+	+
M533 a *G ME MG ma ad* (W) *pn in*	min. & lge.	med.	+	+
M534 a *g ME MG MA AD* (W) *PN IN*	min.	lge.	−	+
M535 a *g me MG MA AD* (W) *PN IN*	min.	min.	−	−
M536 a *g ME mg ma ad* (P) *pn in*	min.	med.	−	+
M537 a *G ME mg MA AD* (W) *pn in*	min.	med.	+	+
M538 a *g me mg MA* ad (P) *PN IN*	min.	min.	−	−
M539 a *G me MG ma AD* (W) *PN IN*	min.	min.	+	−
M540 ? *G ME MG MA AD* (W) *pn IN*	med.	min.	+	+
M541 ? *G ME MG MA AD* (W) *pn IN*	med.	min.	+	+
M542 ? *G ME MG MA AD* (W) *pn in*	med.	min.	+	+
M543 ? *G* me_{12} *MG MA ad* (W) *PN in*	med. & min.	min.	+	+17
M544 a *G me MG MA ad* (W) *PN IN*	lge.	no growth	+	−
M545 a *G ME MG MA AD* (W) *pn IN*	med.	med.	+	+
M546 a *G me MG MA ad* (W) *pn in*	med.	no growth	+	−
M547 a *G ME MG MA AD* (W) *PN in*	med. & lge.	med.	+	+
M548 a *G ME MG ma ad* (P) *PN in*	med.	med.	+	+
M549 a *G me MG MA ad* (P) *PN IN*	lge.	min.	+	−
M550 a *g ME mg ma AD* (W) *pn IN*	min.	med.	−	+
M551 a *g me* mg_3 *MA AD* (W) *pn in*	min.	min.	−	−
M552 a *G ME mg MA AD* (W) *PN IN*	med. & lge.	med. & lge.	+	+
M553 a *G ME MG MA AD* (W) *pn IN*	min. & lge.	med.	+	+
M554 a g_5 me_4 *MG MA ad* (W) *pn in*	min.	no growth	+7	−
M555 a *G* me_4 *MG ma AD* (W) *PN IN*	min.	no growth	+	−
M556 a *g ME* mg_5 *ma ad* (P) *pn IN*	min.	med.	−	+
M557 a *g ME mg MA ad* (P) *PN IN*	min.	min.	−	+
M558 a *G me mg ma AD* (W) *pn IN*	med.	min.	+	−
M560 a *G ME mg MA AD* (W) *PN IN*	med.	med..	+	+
M561 a *g me MG* ma_5 *ad* (W) *pn in*	min.	no growth	−	−
M562 a *G ME MG MA ad* (W) *PN in*	lge.	lge.	+	+
M563 a *G ME MG MA AD* (W) *pn IN*	lge.	lge.	+	+
M564 a *G ME MG MA AD* (W) *PN IN*	med.	min. & lge.	+	+
M565 a *G me MG MA AD* (W) *PN in*	med.	no growth	+	−
M566 a *G ME MG MA AD* (W) *PN in*	min. & med.	med.	+	+
M567 a *G ME MG MA AD* (W) *PN IN*	med.	lge.	+	+
M568 a *G ME MG MA ad* (P) *PN IN*	med.	med.	+	+
M569 a *G ME MG ma AD* (W) *pn in*	med.	med.	+	+

fermenter colonies of two size classes in the same plate. However, the fact that when only minute colonies occur on a plate, they are generally non-fermenters indicates that the genotype is intrinsic in the spore from which the clone descended.

The uniformity in size of pour-plate colonies in a large number of tetrads is, in itself, strong evidence that mutations with regard to fermentative ability did not occur with sufficiently high frequency to be detectable in the microcolony.

In determining the fermentative abilities of the minute colonies, large numbers of them were inoculated into the same broth tube to establish their phenotype with greater certainty. This is especially important when the corresponding glucose slant clone is a non-fermenter. The use of a large number of minute colonies insures that corroboration of the non-fermenter phenotype from glucose was not coincidental. On the other hand, the extra-fermenters in a tetrad would have been diagnosed as such if only a single mutation *(g* to *G; me* to *ME)* occurred on a slant; or, if there were a single fermenter colony amidst the more numerous non-fermenter colonies and this exceptional one were inoculated into sugar broth together with its sister, non-fermenter colonies.

To test for variation among the individual colonies on a plate in the tetrads with extra-fermenters, the following experiment was performed: Two representative tetrads having extra-fermenters were selected (M532–M535; M544–M547) and the clones known to be galactose- and melibiose-fermenters were plated out in glucose nutrient agar directly from the original glucose slant. Ten individual colonies picked at random from each plate were inoculated each into a separate galactose (or melibiose) Durham fermentation tube. All tubes contained gas within 24 hours. This experiment indicates that individual colony variation as regards galactose and melibiose fermentations did not occur in the pour-plate. It also confirms the fact that after an originally recessive, non-fermenter clone has acquired fermentative ability (and thus become the extra-fermenter in the tetrad) this new capacity is not affected by an intervening period of growth on glucose.

Tetrads M488–M491 and M500–M503 (table II) exemplify a situation one would expect as a corollary to the cases of the extra-fermenter tetrads discussed above. The haplophase parents C1A and 607 involved in the crosses analyzed in tables I, III and V are members of the "converting pedigree" and bear the dominant *G* and *ME* alleles. The occurrence of extra-fermenters in these crosses has been explained above as being due to a transfer of gene material from the *G* to the *g (*or *ME* to the *me)* allele. However, 609 (a parent of M488-M503, table II), which is also a member of the "converting pedigree," bore the recessive *me* allele and was mated to a *ME* clone (3190) derived from a regularly segregating *(ME/me)* pedigree. Tetrads M488–M491 and M500–M503 obtained from this cross include more than the two expected *me* clones, indicating that the recessive allele in the converter, i.e., in 609, can degrade the *ME* allele of its mate which descended from a pedigree in which the *ME/me* alleles segregate regularly. At the same time an excess of *G* phenotypes are produced in the same asci.

The occurrence of three non-fermenter segregants in each tetrad is explained on the following basis: During meiosis the *me* gene from the converter parent acquires some essential gene component from the homologous dominant allele of its mate (3190). This acquisition is not sufficient to elevate the *me* allele to functional activity, but the degradation of the *ME* gene is sufficiently severe to negate its normal function. The single fermenter segregant in each tetrad was presumably not affected or, at least, was apparently not degraded below the critical threshold.

TABLE II

TETRAD ANALYSIS OF CONVERTER BY STANDARD HYBRID ASCI, 609 BEING THE CONVERTER

(609 *α G me MA AD*(W) *TH IN py pn* × 3190 a *g ME ma ad*(P) *th in PY PN*)

Tetrad phenotypes									Size of colonies in pour-plates		Fermentation by inocula from pour-plates	
Inocula derived from glucose slants									Gal. plates	Mel. plates	Gal plates to gal. broth	Mel. plates to mel. broth
M488	*α*	*G*	*me*	*MA*	*AD*	(W)	*TH*	*in*	med.	no growth	+	—
M489	*α*	*G*	*me*	*MA*	*AD*	(W)	*TH*	*IN*	med.	no growth	+	—
M490	a	*G*	*me*	*MA*	*AD*	(W)	*TH*	*IN*	med.	no growth	+	—
M491	a	*G*	*ME*	*ma*	*AD*	(W)	*th*	*in*	med.	med.	+	+
M492	*α*	*G*	*ME*	*MA*	*AD*	(W)	*TH*	*in*	med. & lge.	med.	+	+
M493	a	*G*	*me*	*MA*	*ad*	(W)	*TH*	*IN*	med. & lge.	min.	+	—
M494	a	*G*	*me*	*ma*	*ad*	(W)	*th*	*in*	med. & lge.	min.	+	—
M496	a	*G*	*ME*	*MA*	*AD*	(W)	*TH*	*IN*	med.	lge.	+	+
M497	*α*	*g*	*me*	*MA*	*ad*	(W)	*th*	*in*	no growth	min.	—	—
M498	*α*	*g*	*me*	*MA*	*ad*	(W)	*th*	*in*	no growth	min.	—	—
M500	*α*	*G*	*me*	*MA*	*ad*	(P)	*TH*	*IN*	min. & med.	min.	+	—
M501	a	*G*	*me*	*MA*	*ad*	(W)	*th*	*in*	med.	no growth	+	—
M502	*α*	*G*	*ME*	*MA*	*ad*	(P)	*TH*	*in*	med.	med.	+	+
M503	a	*g*	*me*	*MA*	*ad*	(W)	*th*	*in*	min.	min.	—	—

TABLE III

TETRAD ANALYSIS OF CONVERTER BY STANDARD HYBRID ASCI, 607 BEING THE CONVERTER

(607 a *G ME ma AD*(W) × 3168 *α g me MA ad*(P))

Tetrad phenotypes							Size of colonies in pour-plates		Fermentation by inocula from pour-plates	
Inocula derived from glucose slants							Gal. plates	Mel. plates	Gal. plates to gal. broth	Mel. plates to mel. broth
M508	?	*G*	*ME*	*ma*	*ad*	(W)	med.	med.	+	+
M509	?	*g*	*ME*	*ma*	*ad*	(W)	no growth	med.	—	+
M510	?	*G*	*ME*	*MA*	*AD*	(W)	lge.	med.	+	+
M511	?	*G*	*ME*	*MA*	*AD*	(W)	lge.	med.	+	+
M512	?	*G*	*ME*	*ma*	*AD*	(W)	lge.	lge.	+	+
M513	?	*G*	*ME*	*ma*	*ad*	(W)	lge.	lge.	+	+
M514	?	*g*	*ME*	*MA*	*AD*	(W)	min.	med.	—	+

TABLE IV

TETRAD ANALYSIS OF CONVERTER BY STANDARD HYBRID ASCI, 608 BEING THE CONVERTER

(608 a *g me mg* S *MA AD*(W) *TH IN PN py* × M317 *α G ME MG* S *ma ad*(P) *th in pn py*)

Tetrad phenotypes	Size of colonies in pour-plates		Fermentation by inocula from pour-plates	
Inocula derived from glucose slants	Gal. plates	Mel. plates	Gal. plates to gal. broth	Mel. plates to mel. broth
M591 α *G me* MG S *MA AD* (W) *TH IN pn py*	med.	min.	+	—
M592 a *G me* MG S *MA ad* (W) *th in pn py*	med.	no growth	+	—
M593 a *G me mg* S *MA ad* (W) *th in pn py*	med.	no growth	+	—
M594 α *g me mg* S *MA AD* (W) *TH IN pn py*	no growth	min.	—	—
M595 a *G me* mg_3 S *MA AD* (W) *TH IN pn py*	min. & med.	min.	+	—
M596 a *G me* MG S *MA AD* (W) *TH IN PN py*	med.	min.	+	—
M597 α *g me mg* S *MA ad* (W) *th in pn py*	min.	no growth	—	—
M598 α *G me mg* S *MA ad* (W) *th in pn py*	min. & med.	no growth	+	—
M599 a g_5 *me* MG S *MA ad* (W) *th in pn py*	med.	min.	+[6]	—
M600 a g_7 *me* MG S *MA AD* (W) *TH IN pn py*	med.	min.	+[6]	—
M601 α *G me mg* S *MA ad* (W) *th in PN py*	med.	no growth	+	—
M602 α *G me mg* S *MA ad* (W) *th in pn py*	lge.	no growth	+	—
M603 α g_5 *me mg* S *ma AD* (W) *TH IN PN py*	med.	min.	+[5]	—
M604 a *G me* mg_6 S *MA ad* (W) *th in pn py*	lge.	no growth	+	—
M605 α *g me* MG S *ma ad* (W) *th in pn py*	min.	no growth	—	—
M606 a g_4 *me* mg_4 S *MA AD* (W) *TH IN PN py*	med.	min.	+	—
M607 a *G me* MG S *MA AD* (W) *TH in pn py*	med.	min.	+	—
M608 a *G me mg* S *MA AD* (W) *TH IN pn py*	med.	min.	+	—
M609 α g_7 *me mg* S *MA ad* (W) *th in pn py*	med.	no growth	+[8]	—
M610 α *g me* MG S *MA ad* (W) *th in pn py*	min.	no growth	—	—
M611 α *G me mg* S *MA ad* (W) *th in pn py*	lge.	no growth	+	—
M612 a g_5 *me* mg_5 S *ma ad* (W) *th in pn py*	med.	no growth	—	—
M613 a *G me* mg_4 S *MA AD* (W) *TH IN pn py*	lge.	min.	+	—
M614 α *G me* MG S *MA AD* (W) *TH IN pn py*	med.	min.	+	—
M615 a *G me* MG S *MA AD* (W) *TH IN PN py*	lge.	min.	+	—
M616 α *G me mg* S *MA ad* (W) *th in pn py*	med.	min.	+	—
M617 a g_7 *me* MG S *ma ad* (W) *th in pn py*	med.	min.	+[6]	—
M618 α *G me mg* S *MA ad* (W) *th in pn py*	lge.	min.	+	—
M619 a g_6 *me* MG S *MA ad* (W) *th in pn py*	med.	min.	+	—
M620 α *G me* MG S *MA AD* (W) *TH IN pn py*	lge.	min.	+	—
M621 a g_8 *me mg* S *MA ad* (W) *th in pn py*	med.	no growth	+[9]	—
M622 α *g me mg* S *ma AD* (W) *TH IN PN py*	min.	no growth	—	—
M623 α *g me* MG S *MA AD* (W) *TH IN pn py*	min.	min.	—	—
M624 α *G me mg* S *MA ad* (W) *th in pn py*	lge.	no growth	+	—
M625 a *G me mg* S *MA AD* (W) *th IN pn py*	lge.	no growth	+	—
M627 a *g me* MG S ma_5 *ad* (W) *th in pn py*	no growth	no growth	—	—
M628 a *G me mg* S *MA ad* (W) *th in pn py*	lge.	min.	+	—
M629 α *g me mg* S *MA AD* (W) *th in pn py*	min.	min.	—	—
M630 α *g me* MG S *MA AD* (W) *TH IN pn py*	no growth	no growth	—	—
M631 a *G me* MG S *MA ad* (W) *th in pn py*	lge.	no growth	+	—
M632 α *G me mg* S *MA ad* (W) *th in pn py*	lge.	min.	+	—
M633 α g_7 *me mg* S *MA AD* (W) *TH IN PN py*	med.	min.	+[7]	—

TABLE V

TETRAD ANALYSIS OF A CONVERTER BY STANDARD HYBRID ASCI, *C1A* BEING THE CONVERTER

(*C1A a G ME S MG MA AD TH IN PN py* × 5859 a *g ME s MG MA AD TH IN PN PY*)

Tetrad phenotypes		Fermentation by inocula from pour-plates
Inocula derived from glucose slants	Size of colonies in gal. pour-plates	Gal. plates to gal. broth
M464 *a G ME s MA MG TH py*	large	+
M465 *a G ME S MA MG TH py*	large	+
M466 a *G ME S MA MG TH PY*	medium	+
M467 a *G ME S MA MG TH PY*	medium	+
M468 *a G ME s MA MG TH py*	medium	+
M469 a *G ME S MA MG TH PY*	medium	+
M470 *a g ME S MA MG TH py*	minute	−
M471 a *g ME S MA MG TH PY*	minute	−
M472 a *G ME s MA MG TH PY*	large	+
M473 *a G ME S MA MG TH PY*	large	+
M474 *a G ME S MA MG TH py*	large	+
M475 a *G ME S MA MG TH py*	large	+
M476 a *G ME S MA MG TH PY*	medium & large	+
M477 *a G ME S MA MG TH PY*	medium	+
M478 a *G ME S MA MG TH py*	medium	+
M479 *a G ME S MA MG TH py*	medium	+
M480 a *G ME S MA MG TH PY*	large	+
M481 *a g ME S MA MG TH PY*	no growth	−
M482 *a G ME S MA MG TH PY*	large	+
M484 *a G ME s MA MG TH py*	medium	+
M485 *a G ME S MA MG TH PY*	medium	+
M486 a *G ME S MA MG TH py*	medium	+

Even more striking instances of gene degradations are evident in clones M591 to M633. In contrast to the mating 609 × 3190, which involved the melibiose gene as the only recessive converter among the sugar markers used, mating 608 × M317 (table IV) involved four heterozygous sugar markers with the converter parent carrying the recessives *g*, *me*, and *mg*. The total absence of progeny capable of producing gas from melibiose in the Durham tubes in all the tetrads derived from this cross is notable, and is perhaps indicative of a marked instability of the dominant gene controlling the fermentation of melibiose. It is also interesting that, with one exception, each tetrad comprises two clones yielding minute colonies in melibiose pour-plates and two showing no growth. Three tetrads from the same cross also include a deficiency of *G* clones, while three other tetrads include an excess of *G* segregants. The absence of any 4:0 *G*:*g* tetrads is significant. In addition, 10 "slow"-fermenters of galactose were obtained.

The converter 608 carried the dominant *MA* allele, and tetrads obtained by mating this clone to M317 (which carried the recessive, *ma*) generally comprise an excess of maltose fermenters (usually 4:0). Similar cases of 4:0 segregations when

the converter parent carried dominant alleles for fermentative ability can be seen in other crosses.

The significant point is that the phenomenon is non-specific. That is, the presence of the recessive gene in a converter parent need not always result in tetrads with an excess of recessive progeny, for it is conceivable that the dominant allele may not necessarily be completely degraded. The recovery of 4:0, fermenter: non-fermenter progeny from crosses of dominant converters by recessive, standard clones suggests that the dominant gene in the converting parent is not degraded so severely as in cases involving crosses of dominant, standard clones by recessive converters. Converter haploids may thus differ from standard haploids in possessing a more pronounced lability of the genotype, although the detection of truly non-Mendelian segregations in crosses involving two standard clones is by no means rare.

The data presented above eliminate the possibility that non-Mendelian tetrads arise from mutations during the growth of originally Mendelian tetrads on glucose. The exclusion of mutations as a possible cause of irregular ratios leaves open polysomy and polyploidy as possible mechanisms. Rather, the data suggest that irregular segregations of the abilities to ferment galactose and melibiose may originate in the heterozygous condition owing to gene conversions.

NON-MENDELIAN SEGREGATIONS AT OTHER LOCI

The view that non-Mendelian ratios arise from gene conversions in the heterozygote rather than from chance mutations has been confirmed above only with respect to galactose and melibiose fermentations. No attempt was made to verify irregular ratios of other sugar markers (sucrose, alpha methyl glucoside, and maltose) using pour-plates of tetrads as checks. The widespread irregular segregations of these markers suggests, however, that conversion of alleles was operative here also.

A few "slow"-fermenter clones are listed in tables I and IV. "Slow" fermentation of galactose was analyzed in a previous report (Mundkur and Lindegren, 1949) where it was shown to result from selection in galactose broth of *G* mutants descended from originally *g* segregants. In the present analyses, no attempt was made to determine whether the "slow" fermenters are similar to those previously analyzed or result from a delayed phenotypic expression of gene conversions because of the obvious difficulties involved in making such a distinction.

Segregations of vitamin-synthesizing abilities were also irregular, exceptional tetrads occurring with higher frequency than are encountered in standard pedigrees. Table VI summarizes the frequency of irregular tetrads.

TABLE VI

NON-MENDELIAN INHERITANCE OF VITAMIN-SYNTHESIZING ABILITIES IN TETRADS SHOWN IN TABLES I TO V. ONLY 4-SPORED AND OBVIOUSLY NON-MENDELIAN 3-SPORED ASCI ARE INCLUDED.

Vitamin	Number of heterozygous asci marked for the vitamin	Frequency of non-Mendelian asci
Thiamin	11	4
Inositol	20	7
Pantothenate	19	11
Pyridoxine	5	2

In addition to the disturbances in segregations of sugar markers, the irregularities in inheritance of adenine-synthesizing ability are very pronounced. It has been shown (Lindegren and Lindegren, 1947) that pink haploids result from the inability to synthesize adenine and that white clones are generally adenine-independent. Occasional tetrads with excess of white progeny out of a pink × white mating have been interpreted as being due to depletions of pinks. The pink color was restored to activity following outcrosses.

The irregular ratios for the *AD*(W)/*ad*(P) alleles in the present analyses are presumably conditioned by the same mechanism. Several tetrads shown in the tables comprised four white progeny out of a pink × white cross but in some, two clones are *ad*(W) and two are *AD*(W). This fact further confirms the hybridity of the asci analyzed.

Disturbances in mating reactions are also noteworthy. In testing for mating type specificity, a heavy inoculum of each of the four segregants from a tetrad is held in glucose broth together with a standard *α* clone known to copulate vigorously with other haploids. A positive mating reaction identifies its mate as an "a" mating type; in the absence of copulations, the mate is diagnosed as a clone of like mating type, i.e., as an *α* mating type. Copulations are generally effected within a few hours. In the present analyses, mating type specificity segregated 2a/2*α*. Occasional disturbances in mating reactions were, however, encountered. For instance, tetrad M528–M531 (W W W W) was mated to the standard *α* clone but no copulations were observed until the fifth day; tetrads M536–M539, and M548–M551 (2 P:2 W) had the normal mating strength and copulated vigorously within twelve hours. Other tetrads (table I), none of whose haplophases copulated with the standard *α* clones even on the fifth day, were subsequently mated with a standard a clone, and two of the haplophases from each of these tetrads copulated vigorously. Still others, M540–M543 (table I) and M508–M514 (table III) mated with neither the *α* nor the a standard clones. Similar instances of W W W W tetrads failing altogether to copulate are cited in Lindegren (1949) and Mundkur and Lindegren (1949).

The fact that mating strength is normal in 2 P:2 W asci but is impaired or absent in some W W W W asci (obtained from P × W crosses) suggests that the phenomenon is in some way associated with disturbances at the *AD/ad* loci. Further investigation of mating type reactions was not undertaken.

DISCUSSION

Winkler's (1930, 1932) proposal of the Konversions-Theorie was an attempt to explain deviations from the expectations of tetrad analysis which could not be satisfactorily explained by the theory of crossing-over. Winkler's 1932 paper is the most ambitious attempt at refuting arguments levelled against his theory by Stern (1930, 1931, 1932), who insisted that the deviations cited by Winkler did not invalidate the theory of crossing-over.

Winkler's Konversions-Theorie postulates a physiological transition of the gene from one physiological condition to another during the maturation divisions. According to him, "monogenic" conversions involve the transformation of the recessive gene alone into a dominant one; or a transformation of the dominant alone into the recessive condition. When, however, the recessive gene acquired dominance while, simultaneously, the dominant allele transformed into recessiveness, the conversion was "digenic." The experiments reported in the present paper have justified Winkler's insistence on the necessity of performing tetrad analyses as a means of determining whether irregular segregations arise from conversions or exclusively from cross-overs or other chromosomal aberrations. However, owing to the precision with which the crossing-over theory can predict map distances, his view that conversions can explain all cases interpreted as cross-overs seems far fetched. When adequate tetrad analyses are available it is possible to distinguish those cases involving conversions from those involving crossing-over. Monogenic conversions can be detected unambiguously when segregations in a monohybrid tetrad show unequal frequencies of the dominant and recessive genes. It is simpler to assume that what Winkler termed digenic conversions are actually cross-overs since the results of this phenomenon lead so clearly to the prediction to map distances.

Zickler (1934) made exhaustive genetical investigations on the heterothallic ascomycete *Bombardia lunata.* Tetrad analyses of pedigrees heterozygous for *rubiginosa/viridis* revealed high frequencies of non-Mendelian ratios among several thousands of asci. Such exceptional asci contained spore tetrads exhibiting 6:2 and 8:0 *rubiginosa/viridis* segregations. These markers involved spore color and, though morphological, the characters could be distinguished from each other with great precision, in contrast to many morphological markers whose diagnosis is often ambiguous. To explain deviations in segregations from the Mendelian expectations in *B. lunata,* Zickler invoked the Konversions-Theorie and held that crossing-over cannot explain the *monogenic* conversions encountered.

Wülker (1935) analyzed numerous crosses in *Neurospora sitophila,* and observed significant divergences from Mendelian expectations. He described perithecia in which the asci exhibited either a 4:4, 0:8, or 2:6 segregation, exclusively; other

perithecia—the so-called "Mischperithecien"—in which all these three ascus types occurred were also found. The high frequencies of irregular segregations he discovered are evident from his data for the mixed perithecia:

4:4 segregations = 30 asci (19.9 per cent)
2:6 segregations = 92 asci (60 per cent)
0:8 segregations = 29 asci (19.2 per cent)

Perithecia showing only one ascus type:

4:4 segregations = 0 asci
0:8 segregations = 89 asci

However, in spite of these discrepancies, Wülker could not decide in favor of any one of the three explanations for divergent asci he suggested as possible: the labile nature of the gene, conversions, and the influences of environmental factors. This, indeed, is not surprising for he investigated only a single pair of markers L/l (the formation of *Luftmyzel* or its absence) in the non-Mendelian pedigrees.

In addition to the non-Mendelian segregations discovered in *Bombardia* and *Neurospora,* numerous instances of exceptions to Mendelian ratios are known in the fungi. Such irregularities occur in *Coprinus fimetarius* (Brunswik, 1926); *Ustilago levis* (Dickinson, 1928); *Aleurodiscus* (Kniep, 1928); *Phycomyces blakesleeanus* (Burgeff, 1928); *Ustilago zeae* (Hanna, 1929; Christensen, 1931); *Sphacelotheca* (Rodenhiser, 1932); *Sphaerocarpus* (Allen, 1930); *Hypomyces Ipomoeae* (Dimock, 1939). However, in none of these fungi are chromosome maps available; and these are required to distinguish actual non-Mendelian segregations from aberrant ratios arising from segregations of polymeric hybrids or from segregations of hybrids carrying duplications.

The unique advantages of tetrad analysis are obvious, and it is not surprising that irregular segregations are encountered more frequently in the fungi, where tetrad analysis is feasible, than in higher organisms, where it is not. When higher organisms are used as genetic material, the conclusive detection of irregular segregations is either impossible or the chances of detecting true conversions are, at best, greatly reduced. This limitation derives from the fact that since tetrad analysis is not possible in these organisms regular gametic segregations have been *assumed* to occur. During animal oogenesis, for instance, a regular 2:2 segregation of genes among the nucleus in the egg cell and the three polar bodies is only *inferred* provided an approximately 1:1 ratio is obtained when a heterozygous female is mated to a recessive male. Similar inferences are also made with regard to microsporogenesis and megasporogenesis in higher plants. These inferences regarding the ratios of segregations among the gametes can be based only on the recombinations of the markers in the F_1 generation since the products of meiosis are not directly accessible for characterization. Apparent instances of irregular segregations can be explained on the basis of ploidy or crossing-over if they can be verified by cytological methods. However, significant deviations from 1:1 segregations among the progeny of a hybrid higher plant or animal are *assumed* to be

due to preferential survival of sperm or eggs carrying the dominant allele, or to some chromosomal aberration.

Tetrad analyses of all the nuclei originating from the same mother cell have, in yeast, yielded vital information inconsistent with the assumptions and inferences involved in the genetical analyses of higher plants and animals. A knowledge of linkage groups in *Saccharomyces* has been of especial usefulness.

The necessity for tetrad analysis in evaluating the status of non-Mendelian inheritance lies in the accessibility to *all* the haploid products of meiosis for a *direct* characterization. Unlike higher organisms where the F_1 generation is analyzed, tetrad analysis in the fungi is not obscured by dominance effects or by the ambiguities concerning survival of the products of reduction or of competitions between them resulting in selective fertilization. Moreover, when enough markers are employed, recourse to tetrad analysis makes genetical characterizations of large numbers of progeny a relatively unimportant matter. When biochemical criteria are used, as in the present investigation, tetrad analysis acquires an added significance. Segregations of abilities or inabilities to ferment various sugars, synthesize vitamins and other cell components are gene-controlled and can therefore be diagnosed without ambiguity. Where the recessive markers used are especially "good" (examples: *g, me, ma, mg, ad, th, in, pn, py*) the segregations are exceptionally clear-cut.

TABLE VII

EXPECTATIONS OF DOMINANT AND RECESSIVE PHENOTYPES WHEN DOUBLE DOMINANT OR DOUBLE RECESSIVE DISOMICS (*PP; pp*) ARE CROSSED WITH NORMAL, HAPLOID CLONES OF OPPOSITE PHENOTYPE

Mating	Type of ascus	Ratio of phenotypes (dominants : recessives) *Pp* genotype = *P* phenotype	Frequency
PP × *p*	(a) *PP PP p p*	2 : 2	1
	(b) *PP P pP p*	3 : 1	4
	(c) *PP P p pP*	3 : 1	
	(d) *P PP pP p*	3 : 1	
	(e) *P PP p pP*	3 : 1	
	(f) *P P pP pP*	4 : 0	7
pp × *P*	(a) *Pp Pp p p*	2 : 2	1
	(b) *Pp P pp p*	2 : 2	1
	(c) *Pp P p pp*	2 : 2	1
	(d) *P Pp pp p*	2 : 2	1
	(e) *P Pp p pp*	2 : 2	1
	(f) *P P pp pp*	2 : 2	1

Among the objections raised against a gene-component transfer mechanism as an explanation for non-Mendelian inheritance, polysomy and polyploidy (Lederberg, 1948) are noteworthy. Such mechanisms, if they were operative in producing irregular ratios in *Saccharomyces*, would yield the phenotypes shown in tables VII and VIII. If we designate a dominant phenotype by *P*, and its alternative, recessive manifestation by *p*, tetrad analysis of the crosses $PP \times p$ (where *PP* is the disomic[1] double dominant parent) and $pp \times P$ (where *pp* is the disomic parent) should yield the tetrad types designated in table VII.

On the other hand, if a *Pp* disomic haploid originating from a heterozygous *(P/p)* diploid were crossed to a standard haploid clone of opposite phenotype the following tetrad types should result:

TABLE VIII

EXPECTATIONS OF DOMINANT AND RECESSIVE PHENOTYPES WHEN A *Pp* DISOMIC IS CROSSED WITH A NORMAL HAPLOID CLONE OF CONTRASTING PHENOTYPE

Mating	Type of ascus	Ratio of phenotypes (dominants : recessives) *pP* genotype = *P* phenotype	Frequency
$Pp \times p$	(a) *pP pP p p*	2 : 2	1
	(b) *pP p pP p*	2 : 2	1
	(c) *pP p p pP*	2 : 2	1
	(d) *p pP pP p*	2 : 2	1
	(e) *p pP p pP*	2 : 2	1
	(f) *p p pP pP*	2 : 2	1

A comparison of the frequencies of ascus types expected on the basis of polysomy shown in tables VII and VIII with the frequencies actually encountered in the five crosses described (tables I–V) shows obvious discrepancies. The possibility of a *pp* disomic effecting the irregularities is precluded by the occurrence of frequent deviations in segregation ratios in heterozygous crosses where the converter parent carried the recessive phenotype, although the only ratio expected (if a *pp* disomic parent were involved) is 2:2. The most striking divergences are seen in table IV where a 0:4 melibiose fermenter:non-fermenter ratio is the only one encountered; at no locus is there the required consistent 2:2 segregation in crosses where the converter carried the recessive phenotype. The possibility of a *Pp* disomic is also negated for the same reason since a 2:2 segregation would invariably be expected if such a disomic were involved in a cross with a normal haploid of contrasting phenotype. On the other hand, there is a significant deviation from the ratios expected if a *PP* parent were involved.

[1] The term "trisomic" describes diploid organisms having an extra chromosome. Since this term was coined particularly for normally *diploid* organisms, the term "disomic" may be used to describe a *haploid* individual bearing an extra chromosome.

TABLE IX

DISTRIBUTION OF TETRADS PRODUCED IN RECESSIVE CONVERTER × STANDARD DOMINANT CROSSES

(Only hybrid asci heterozygous for sugar markers that were recessive in the converter parents (tables II and IV) are included. The occurrence of unpredicted tetrad classes makes statistical analysis irrelevant and excludes the possibility that polysomy in the haploid parents is involved.)

Ratio of fermenter:non-fermenter phenotypes	Observed frequencies			Per cent of expected frequencies
	Gal.	Mel.	α Methyl gluc.	
2:2	2	0	6	100
0:4	0	9	0	0
1:3	3	2	3	0
3:1	4	0	0	0

TABLE X

SUMMARIZED DISTRIBUTION OF TETRADS PRODUCED IN DOMINANT CONVERTER × RECESSIVE STANDARD CROSSES

(Only those hybrids heterozygous for sugar markers (tables I to V) are included. Significant deviations from expected ratios for galactose and melibiose markers exclude polysomy in the dominant converter parents.)

Ratio of fermenter:non-fermenter phenotypes	Observed frequencies				Per cent of expected frequencies
	Gal.	Mel.	Malt.	α Methyl gluc.	
2:2	4	4	3	1	8.33
3:1	4	3	8	2	33.33
4:0	7	2	8	4	58.33
1:3	0	0	0	1	0
χ^2 =	9.8	15.5	2.51		
P value =	<.01	<.001	<.30		

Polyploidy is only an extension of polysomy in that every linkage group is represented more than once in an ascospore, while in disomy only one linkage group is represented twice in an ascospore. Some markers in the present analyses belong in different linkage groups (for example, mating type specificity and abilities to synthesize pantothenate and ferment galactose are determined by genes located in separate chromosomes). However, the fact that in the same ascus some markers segregate in a precisely Mendelian manner while others segregate irregularly is *a priori* evidence for the exclusion of polyploidy as the mechanism yielding irregular ratios. Lindegren (1949a) has shown that the concept of modifying genes is inadequate to explain irregular segregations in yeasts. In the present analyses, polymeric genes affecting melibiose fermentative ability are excluded by the occurrence of non-fermenter progeny among the offspring of 608, a non-fermenter converter.

The transformed (converted) recessive haplophase clones maintain the transformed type through successive sub-culture generations, within the limits imposed by a normal mutation rate; since back mutations of transformed recessives (e. g., *me* to *ME*) do not occur in excess of expectation among the segregants recovered from a hybrid, the transformation of *ME* to *me* is not of the type already described as depletion mutation.

The high frequencies of non-Mendelian segregations discovered in the present work derive from the use of parent stocks especially conducive to evoking irregular ratios; exceptional ratios that can be interpreted only on a basis of gene conversions are, however, by no means rare even in some so-called regularly segregating pedigrees. The complete loss of ability to ferment melibiose among the offspring of a culture capable of vigorous fermentation of the sugar—a phenomenon not recorded previously—is difficult to explain on the basis of the Plasmagene Theory, and questions a long-held genetical tenet: the integrity of the gene as a Mendelian unit uncontaminable in the heterozygote.

SUMMARY

Tetrad analyses of five different crosses of *Saccharomyces* haploids with the use of biochemical markers revealed high frequencies of irregular segregation ratios. These irregularities derived from the use of certain haplophase parent stocks which, when crossed to standard haplophase clones, produced marked disturbances in segregations in the progeny. Clones effecting such disturbances have been designated as "converters."

These findings are contrary to the regular 1:1 gametic segregations expected by conventional Mendelian genetics.

In heterozygous crosses, when converter parents carrying dominant, fermenter phenotypes were mated to clones obtained from standard pedigrees, the progeny comprised an excess of fermenter segregants. Converter parents carrying the recessive, non-fermenter phenotypes, when crossed with standard clones of contrasting phenotype, yielded tetrads frequently comprising an excess of non-fermenter segregants.

Irregularities in segregation of vitamin-synthesizing abilities, and disturbances in mating type specificity were also encountered.

These experiments have yielded data that are not amenable to adequate interpretation on the bases of the established concepts of Mendelian genetics. Conversion of alleles in the heterozygote effected by gene-to-gene transfer of gene components has therefore been invoked as an explanation for the anomalies discovered.

ACKNOWLEDGMENTS

I am deeply indebted to Dr. Carl C. Lindegren and Mrs. Gertrude Lindegren for generous facilities and helpful suggestions during the course of this work. I am also thankful to the Trustees of the R. D. Sethna Foundation, Bombay, India, for sponsoring my studies under Dr. Lindegren.

LITERATURE CITED

Allen, C. F. (1930). Gametophytic inheritance in *Sphaerocarpus*. IV. Further studies on tuftedness and polyclady. Genetics **15**:150–188.

Brunswik, H. (1926). Die Reduktionsteilung bei den *Basidiomyzeten*. Zeitschr. f. Bot. **18**:481–498.

Burgeff, H. (1928). Variabilität, Vererbung und Mutation bei *Phycomyces Blakesleeanus*. Zeitschr. f. ind. Abst.-u. Vererbgsl. **49**:26–94.

Christensen, J. (1931). Studies on the genetics of *Ustilago zeae*. Phytopathol. Zeitschr. **4**:129–188.

Dickinson, S. (1928). Experiments on the physiology and genetics of the smut fungi. Cultural characters. I. Their permanence and segregation. Proc. Roy. Soc. Lond. B **103**:547–555.

Dimock, A. W. (1939). Studies on ascospore variants of *Hypomyces Ipomoeae*. Mycologia **31**:709–727.

Hanna, W. F. (1929). Studies in the physiology and cytology of *Ustilago zeae* and *Sorosporium reilianum*. Phytopath. **19**:415–442.

Kniep, H. (1928). Die Sexualität der niederen Pflanzen. Jena.

Lederberg, J. (1948). Problems in microbial genetics. Heredity **2**:145–198.

Lindegren, C. C. (1949). The Yeast Cell. Its Genetics and Cytology. Educational Publ. Inc. St. Louis.

———, (1949a). Chromosome maps of *Saccharomyces*. Hereditas Suppl. Vol., pp. 338–355.

———, and Lindegren, G. (1946). The cytogene theory. Cold Spring Harbor Symp. Quant. Biol. **11**:115–129.

———, ———, (1947). Depletion mutation in *Saccharomyces*. Proc. Nat. Acad. Sci. (U.S.) **33**:314–318.

Monod, J. (1947). The phenomenon of enzymatic adaptation. Growth Symp. **11**:223–289.

Mundkur, B. D., and Lindegren, C. C. (1949). An analysis of the phenomenon of long-term adaptation to galactose by *Saccharomyces*. (Amer. Jour. Bot., in press.)

Rodenhiser, H. A. (1932). Heterothallism and hybridization in *Sphaerotheca sorghi* and S. *cruenta*. Jour. Agr. Res. **45**:287–296.

Spiegelman, S. (1946). Nuclear and cytoplasmic factors controlling enzymatic constitution. Cold Spring Harbor Symp. Quant. Biol. **11**:256–277.

Stern, C. (1930). Konversionstheorie und Austauschtheorie. Biol. Zentralbl. **50**:608–624.

———, (1931). Zytologisch-genetische Untersuchungen als Beweise fur die Morgansche Theorie des Faktorenaustauschs. *Ibid*. **51**:547–587.

———, (1932). Uber die Konversionstheorie. *Ibid*. **52**:367–379.

Winkler, H. (1930). Die Konversion der Gene. 186 pp. Jena.

———, (1932). Konversions-Theorie und Austausch-Theorie. Biol. Zentralbl. **52**:163–189.

Wülker, H. (1935). Untersuchungen über Tetradenaufspaltung bei *Neurospora sitophila* Shear et Dodge. Zeitschr. f. ind. Abst. - u. Vererbgsl. **59**:210–248.

Zickler, H. (1934). Genetische Untersuchungen an einem heterothallischen Askomyzeten (*Bombardia lunata* nov. spec.). Planta **22**:573–613.

EXPLANATION OF PLATE

PLATE I

Melibiose pour-plates of tetrad M532-M535. Three plates (left to right) have colonies each of which is individually capable of fermenting melibiose. Inocula derived from glucose slants corresponding to each clone can also ferment melibiose. Pour-plate of M535 has minute, non-fermenter colonies, and the clone derived from the corresponding glucose slant cannot ferment melibiose. The medium-sized colonies of M533 are not the result of crowding.

M532

M533

M534

M535

NEW SPECIES OF LONCHOCARPUS FROM PANAMA[1]

FREDERICK J. HERMANN
U. S. Department of Agriculture

Three Panamanian collections of *Lonchocarpus* which Dr. Robert Schery was unable to place among the species known from Central America were recently sent to the writer for study. All of them proved to be novelties for that region, as Dr. Schery had concluded: two of them undescribed species, of which the first is represented also in Costa Rica, and the third a tree of British Guiana, as follows:

LONCHOCARPUS **oliganthus**, sp. nov.—Frutex vel arbor gracilis ca. 10 m. alta; folia 5–7-foliolata; foliola oblonga vel elliptica multipunctata petiolulis subquadrangularibus; paniculae axillares 3–4 subspiciformes laxifloraeque foliis multo breviores; pedunculi secundarii minimi uniflori (raro biflori); pedicelli 0.5–0.7 mm. longi; flores 8–9 mm. longi, purpurei; calyx cupuliformis, margine integra vel aliquantum undulata; vexillum late oblongum vel oblongo-ovatum, externe dense argenteo-sericeum, margine valde inflexa; alae oblongae; carinae petala plus minusve falcata marginibus inferioribus solum per intervallum brevissimum apici propinquum connatis; stamen vexillare in fenestra et prope apicem columnae filamentarum liberum; ovarium 5–6-ovulatum; legumen ignotum.

Shrub or slender tree about 10 m. high, 17 cm. in diameter at base, with "dark brown, almost glabrous, shallowly striate bark" (Smith), and terete, glabrous, shallowly and irregularly sulcate branchlets dotted with small but conspicuous lenticels; stipules scale-like, oblong, 1 x 0.7 mm., dark brown, closely appressed; leaves 5–7-foliolate, 18–30 cm. long, the petiole subterete, canaliculate and often sulcate, glabrous or very sparingly strigose, 3.5–6.5 (averaging 4) cm. long, the rachis deeply canaliculate, sparsely strigose to glabrate; petiolules 4.5–6 mm. long, subquadrangular, minutely strigose to glabrous, dark brown to black, more or less canaliculate above; leaflets thin-chartaceous, oblong to elliptic, the blade 6–15 cm. long, 2.5–7 cm. wide, dark green (sometimes paler beneath), faintly but heavily mottled above with purplish brown, copiously strigose when young, at maturity glabrous or minutely and sparingly strigose beneath, multipunctate (each cell with several to many semitranslucent puncta), caudate at the apex, rounded or tapering at the base, the margin minutely crenulate, the lateral veins 9–10 pairs; panicles 3–4, borne singly in the upper leaf-axils, short (6–10 cm. long), much surpassed by the leaves, slender, subspiciform, loosely flowered; primary peduncles subterete to subquadrangular, glabrous or glabrate, slender (1 mm. or less wide at the base), floriferous to within 1.5–4 cm. of the base; secondary peduncles rudimentary, about 0.5 mm. long by 0.7–1 mm. wide, 1-, rarely 2-, flowered (the second flower commonly aborted); bracts and bractlets similar, squamiform, ovate, 0.7–1 mm.

[1]Issued September 30, 1949.

long, densely strigose, the bracts caducous, the bractlets attached near the base of the calyx; pedicels 0.5–0.7 mm. long; flowers 8–9 mm. long, "purple" (von Wedel); calyx cupuliform, 2.5–3 x 3 mm., reddish brown, minutely tawny-strigose, the margin entire or slightly undulate, the teeth, except the broadly deltoid carinal tooth (0.1–0.4 mm. long), obsolete; standard broadly oblong to oblong-obovate, 9 x 7 mm., reflexed, copiously silvery-sericeous without, glabrous and lineate within, "center and margin pale green-yellow enclosing an area of violet" (Smith), deeply emarginate and somewhat cucullate at the apex, the margin strongly inflexed, irregularly truncate at the base, the auricles very short (0.5 mm.), the claw 1.5 mm. long, a short (0.2 mm.) membranaceous crest between each auricle and the claw; wings 9 mm. long (the claw 2.5 mm.), 2.5 mm. wide, oblong, glabrous except for a sericeous median band (0.6 mm. wide), little widened at the blunt apex, the vexillar half of the blade slightly prolonged at the base to form a shallow auricle (0.7 mm.), adnate to the keel near the base; keel petals 8.5 mm. long (the claw 2.5 mm.), averaging 2.5 mm. wide, somewhat falcate, much broadened toward the blunt apex, their lower margins united only at a point below the apex, glabrous except for the lower margin which is increasingly sericeous toward the apex; stamens monadelphous, glabrous, the tube fenestrate at the base with the margins of the opening thickened, the vexillar stamen free at the opening (1 mm.) and also for the terminal 3 mm.; anthers versatile but attached near the base, 2-celled, narrowly elliptic, 0.8 mm. long; ovary compressed, linear, sessile or substipitate, densely white-strigose; ovules 5–6; style strigose at base, glabrous above; stigma capitellate; pod unknown.

PANAMA: PROVINCIA DE BOCAS DEL TORO: Gray Creek, vicinity of Chiriquí Lagoon, Sept. 8, 1941, *H. von Wedel 2634* (MO TYPE, US).

COSTA RICA: PROV. ALAJUELA: open shade in rain forest alt. 850 m., Villa Quesada, San Carlos Canton, Feb. 21 1939, *Austin Smith H 1613* (F, MO).

The small, sericeous flowers of this species, together with the only slightly coalescent keel petals, almost diadelphous androecium, narrowly oblong wings, and inflexed standard, place it in the subdivision of NEUROSCAPHA designated by Pittier as PUBIFLORI. Its nearest ally is *L. parviflorus* Benth., from which it differs in having leaflets which are twice to three times as large, relatively long (6–10, rather than 2.5 cm.), loosely flowered panicles, and larger flowers (8–9, rather than 6, mm. long). The larger leaflets of *L. oliganthus* set it off likewise from the related *L. atropurpureus* Benth., in which the pedicels are also occasionally, though not predominantly, uniflorous, and from this it is further distinguished by having petiolules twice as long, rudimentary secondary peduncles (0.5, rather than 2–3, mm. long), narrower and densely sericeous standard with claw 1.5 instead of 0.8 mm. long, and densely pubescent ovary.

LONCHOCARPUS **calcaratus**, sp. nov.—Arbor 9 m. alta, ramulis crassis verrucosis; stipulae squamiformes, dense strigosae, caducae; folia 9–11-foliolata; foliola subcoriacea, elliptico-lanceolata, epunctata, subtus strigosa; paniculae laterales, 25

cm. longae, axi primario florigeno simplici, valido, recto; axis secundarius 10–18 mm. longus, gracilis, 5–9 florus; pedicelli gracillimi, 5–6 mm. longi, bracteolis subulatis caducis strigosis prope basim calycis praediti; flores 16–17 mm. longi; calyx late cupuliformis vel cyathiformis, margine subintegra vel aliquantum undulata; vexillum orbiculare prope apicem emarginatum externe sparsissime sericeum; alae cymbiformes margine superiore basi leviter lobata; carinae petala oblongo-falcata ad basim lateraliter calcarata marginibus inferioribus vix connatis; stamen vexillare solum in fenestra columnae filamentarum liberum; ovarium 6–7-ovulatum; legumen ignotum.

Tree 9 m. high, with thick, subterete, often warty branches copiously marked with large, coarse lenticels; stipules squamiform, 2 mm. long, membranaceous, densely strigose, caducous; leaves 9- to 11-foliolate, 15–23 cm. long, the subterete petiole 2–5.5 cm. long, shallowly canaliculate, glabrous or glabrescent, the rachis sparsely strigose to glabrate; petiolules 3.5–5 mm. long, verrucose, conspicuously hirtellous, brown or occasionally olive-green, usually deeply but narrowly canaliculate above; leaflets subcoriaceous, elliptic-lanceolate, the blade 3.5–11 cm. long, 2–4 cm. wide, epunctate, glabrous or glabrescent above, strigose beneath, the apex obtuse, the base cuneate to abruptly acute, about 8–10 of the lateral veins prominent, not impressed, the margin entire, indurated; inflorescence lateral, paniculate, 25 cm. long; primary peduncle and rachis stout (3 mm. in diameter near the base), straight, unbranched, angular, very sparingly strigose, floriferous to within 3 cm. of the base; secondary peduncles 10–18 mm. long, slender, strigose, 5- to 9-flowered; bracts squamiform, 1 mm. long, densely strigose, promptly deciduous; pedicels very slender, 5–6 mm. long, strigose, the caducous copiously strigose bractlets subulate, 1 mm. long, attached near the base of the calyx; flowers 16–17 mm. long, "pink" (Allen); calyx broadly cupulate to cyathiform, firmly chartaceous, 3.5–4 x 8 mm., densely sericeous-strigose, the teeth prominent and broadly deltoid in the bud but the margin in anthesis subentire to shallowly undulate except for the apiculate (0.5 mm.) two lower teeth; standard orbicular, 15 x 15 mm., very sparingly sericeous without toward the emarginate apex, otherwise glabrous, the blade truncate to shallowly cordate at the base, the lobes almost obsolete, the cuneate claw covered by two inflexed, fleshy, partly adherent marginal flaps, their free edges meeting in the center; wings 16 mm. long (the claw 4.5 mm.), 7 mm. wide, cymbiform, very sparsely sericeous without toward the apex, adnate to the keel near the base, the vexillar margin abruptly rounded above the claw to form a broad, shallow lobe; keel petals 15 mm. long (the claw 5 mm.), 4 mm. wide, oblong-falcate, their lower margins united for a distance of 2.5 mm., 3.5 mm. below the obtuse to subacute apex, finely sericeous along the lower margin toward the apex, each petal bearing on its outer face an elongate (3 mm. long, 1.5 mm. wide), hollow spur or pocket midway between the margins, beginning 1 mm. forward from the claw; stamens monadelphous, the tube laterally compressed, fenestrate at the base, the vexillar stamen free only at the opening (2 mm.); anthers versatile but attached very near the base, 2-celled, ovate-oblong, 0.8 mm.

long; ovary linear, laterally compressed, densely white-strigose; ovules 6–7; style essentially glabrous; stigma capitellate; pod unknown.

Panama: prov. de cocle: infrequent, El Valle, floor to 1800 ft., April 8, 1947, *Paul H. Allen 4472* (MO type).

The prolonged, several-flowered secondary peduncles of this species in conjunction with epunctate leaflets allocate it in Bentham's section Paniculati—a group otherwise unknown from Middle America but comprising a single species (*L. praecox* Benth.) in Minas Geraes, Brazil, and four species in tropical Africa. Although no material of any species of the section is available for study, it is evident from Bentham's descriptions (even though the 3-line characterization of *L. praecox* leaves much to be desired) that it is more closely related to the Brazilian species than it is to the African members of the section. The illustration of *Lonchocarpus praecox* in Martius' 'Flora Brasiliensis' (Vol. 15, pt. 1, *t. 105.* 1862) depicts a plant with much shorter panicles than those of *L. calcaratus,* much stouter and more prolonged secondary peduncles (these almost equalling the primary in diameter and length), smaller flowers with the calyx sparsely hirtellous and more prominently toothed, and elliptic-oblong, not at all lanceolate, leaflets. The resemblance of the present species is actually much closer to the plate in Martius *(t. 106)* designated as *Lonchocarpus glabrescens* Benth. The figure of the inflorescence in this plate presents a stout and elongated primary floral axis with short and very slender secondary peduncles as in *L. calcaratus,* but such a conspicuously paniculate inflorescence is not in agreement with Bentham's diagnosis *("floribus fasciculatis")* nor with modern collections from the valley of the Amazon which seem to be correctly referred to this species in the light of the original description. In these specimens the primary floral axis is decidedly woody with the characteristic rudimentary secondary peduncles of Bentham's section Fasciculati to which he referred the plant. According to both Bentham's and modern accounts, *Lonchocarpus glabrescens* is, moreover, a liana with flowers having a subrostrate, strongly arcuate keel, usually 10 ovules, and more prominent calyx teeth.

The pronounced hollow spur in the carinal petals of *Lonchocarpus calcaratus* appears to be a feature almost unique in the genus, occurring otherwise, so far as the writer knows, only in *L. lineatus* Pittier of Gautemala. In the latter species the spur is much more shallow, and the two plants have few other characteristics in common.

Lonchocarpus densiflorus Benth.

A member of Bentham's section Fasciculati, a group heretofore not known to be represented in Middle America. The possession of stipellate leaflets by *L. densiflorus* is an anomalous feature readily setting it off from other species.

Panama: provincia de bocas del toro: Laguna de Chiriquí and its neighborhood, Nov.–Dec., 1885, *John Hart 99* (US) (distributed as *L. sericeus*); Almirante, Sept. 12, 1920, *W. W. Rowlee & H. E. Stork 1002* (US) (distributed as *Andira* sp.). canal zone: vicinity of Mindi, Sept. 13, 1947, *Paul H. Allen 5119* (MO, NA).

A FIRST RECORD FOR THE GENUS QUALEA (VOCHYSIACEAE) FROM NORTH AMERICA (PANAMA)[1]

ROBERT W. SCHERY

QUALEA **cymulosa** Schery, n. sp.—Arbor 30 m. alta, ramis junioribus teretibus puberulentis, vetustioribus glabris cortice rimosa et longitudinaliter lenticellata, lenticellis numerosissimis fulvis elevatis; foliis simplicibus plerumque oppositis aut subopppositis aliquando alternatis, 10–15 cm. longis 4–6 cm. latis, integris ellipticis, ad apicem abrupte acuminatis, ad basim angustatis brevi-cordatis coriaceis glabris reticulatis inter nervos laterales; nervis lateralibus ca. 5–7 jugis arcuatis marginaliter confluentibus facere nervum costae parallelum 2–5 mm. ab margine, subtus nervis prominentibus; petiolis ca. 7 mm. longis, supra sulcatis, puberulentis fuscis; stipulis glandulis ovatis crateriformibus callosis ad petiolorum insertionem, duabus glandulis rotundatis inferius ad basin petioli decurrentis; inflorescentia 15 cm. longa 8 cm. lataque, terminali subterminalique, paniculis cymularum trichotomarum cinereo-puberulentis parvi-bracteatis vel subglandularibus; floribus magnis roseis, calcye cinereo-pubescenti coriaceo, 2 lobis lateralibus orbicularibus ca. 4–5 mm. longis, brunneis leviter pubescentibus, 2 lobis intermediis obovatis ca. 7 mm. longis, 1 loba interiora ca. 1 cm. longa, extus dense cinereo-pubescenti intus glabra, calcare bursiculato ca. 6 mm. longo ad basin inserto; petalo 1 obcordato glabro, ca. 2 cm. longo et 2.5 cm. lato apice profunde bilobato; stamine 1 crasso glabro, ca. 9 mm. longo, anthera biloculari; ovario rotundato dense cinereo-hirsuto 3-loculari, loculis biovulatis; fructibus ignotis.

Tall forest tree, the bark of the young (leaf-bearing) twig puberulent and scarcely lenticellate, the bark of the older twig glabrous and very lenticellate. Leaves simple, usually opposite or subopposite but sometimes alternate, glabrous, elliptic, rather abruptly acuminate, narrowed toward the base and briefly cordate at the extreme base, the lateral veins usually 5–7 pairs and confluent a few mm. from the margin into an undulate marginal vein subparallel to the prominent costa; petioles dark, puberulent, sulcate above; stipules apparently modified (at insertion of petiole) into crateriform "glands" with the elevated callous margins light in color, and with 2 smaller globose prominences a few mm. lower down to the side of the subdecurrent petiole. Inflorescence terminal but its lower subdivisions frequently axillary from upper leaves, thrice-compound, paniculate as a whole but the lateral branchings mostly trichotomous and determinate (cymose), bearing at its branches "glands" similar to the stipular ones, the ultimate and penultimate pedicels with small bracts. Flowers large, showy, rose-pink; calyx coriaceous, cinereous-pubescent, 5-parted, the outer (lateral) 2 lobes smaller, flat and lightly pubescent, the next inner 2 more or less coiled into a cylindric form, the innermost markedly curled into a cone-like cylinder about 1 cm. long, bearing at the base a broad but

[1] Issued September 30, 1949.

flattened thick spur about 6 mm. long and 4 mm. broad, this rounded basally; petal solitary, obcordate, about 2 cm. long and 2.5 cm. broad, short-clawed at the base, deeply cleft at the apex, glabrous; stamen solitary, about 9 mm. long, glabrous, thickish, inserted to the side of the petal, bearing terminally a large, fleshy, bilocular anther less than 2 mm. long; ovary densely cinereous-hirsute, completely 3-carpellate, each carpel 2-ovulate; style glabrous, about equalling the stamen; stigma prominent, capitate.

Panama: darien: headwaters of the Río Chico, June 1947, *P. H. Allen 4645* (Mo. Bot. Gard. type).

This new species constitutes the first record of the genus north of South America. It is thus another example of a typically Amazonian plant having a northern range extension into the dense forest of eastern (southern) Panama. The species apparently falls into Warming's section Costatae (Fl. Bras.) of the genus, and as far as can be told from the literature is distinct from all of the multitude of Amazonian species. There is nothing even similar to it in the relatively meager collections of *Qualea* in the herbarium of the Missouri Botanical Garden, but it may resemble certain Brazilian species such as Q. *rupicola* Ducke, to judge from the original description only.

SOME PTERIDOSPERM STEMS AND FRUCTIFICATIONS WITH PARTICULAR REFERENCE TO THE MEDULLOSAE[1]

ROBERT W. BAXTER[2]

Introduction

Theophrastus, one of the first to attempt the classification of plants, recognized as his major groups, trees, shrubs, and herbs. Although this division was long ago realized to be an artificial one it nevertheless provided then, as it does today, convenient categories for different types of plant habit. Since the study of paleobotany involves not only the search for the ancestral types of present-day plants but also attempts to visualize and illustrate the gross appearance of past floras we may still find it convenient to use these major habit groupings in classifying fossil plants.

We now know that the Carboniferous forests were made up of the tree-like *Pitys*, *Cordaites*, *Lepidodendron*, *Sigillaria* and *Calamites*, which attained diameters of several feet and reached 100 feet or more in height. Growing among these trees were numerous plants of creeping, climbing, and shrubby habit, characterized in general by small stems with little or no secondary growth. It is also generally true that this last group (ferns and seed-ferns) had developed large leaves or fronds (megaphyllous) while the larger tree-like plants were generally small-leaved (microphyllous). The term "microphyllous" is used in this paper in a broad sense to include not only the groups lacking leaf gaps but also those living and fossil gymnosperms (Coniferophyta, Arnold, 1948) in which the seeds are stem-borne (Sahni's (1920) Stachysperms) and the leaves are small, simple, linear or fan-shaped growths, borne in dense spirals or whorls on the trunk and branches.

In plant evolution the early development of a single large trunk (tree-like) seems to have some correlation with microphyllous habit, as the development of numerous small branches of equal size (shrubby) may be correlated with megaphyllous form. Accordingly, it seems possible that a classification based on external form and size may, considered in relation to the origin of plant groups, not be entirely without some phylogenetic meaning.[3] As might be supposed, the larger tree-like fossils

---

[1] An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfilment of the requirements for the degree of Doctor of Philosophy in the Henry Shaw School of Botany.

[2] Assistant Professor of Botany, University of Kansas, Lawrence.

[3] While it is not our present intention more than to suggest the possibility of the foregoing statements, there is ample evidence that the Coniferophyta (Ginkgoales, Taxales and Coniferales) have been trees and microphyllous since their origin from the Pityeae and Cordaiteae in Upper Devonian and Carboniferous times (Arnold, 1948). The other groups of Carboniferous trees *(Calamites, Lepidodendron,* etc.) are, on the other hand, represented today by only a few isolated genera in the so-called fern allies. Thus it would seem that the only possible ancestral forms of the megaphyllous gymnosperms, and possibly the angiosperms, must be sought in the shrubby, climbing or herbaceous undergrowth of the Paleozoic forests. In this habit group through profuse equivalent stem ramifications the *telome* units would be provided for the development of the large frond and broad leaf, which when fertile may have evolved into sporophylls or carpels (Wilson, 1942).

Issued September 30, 1949.

have received a proportionate amount of attention and are today relatively well known. On the other hand, while numerous genera and species of the smaller plants have been discovered and described, it is becoming increasingly apparent that the field is open for the discovery of many more. This is due in part to improved techniques and increasing amounts of research material but probably even more to the undoubted greater diversity of the smaller plants. Certainly in many forest areas today, the genera and species of tree-like habit are but a small fraction of the total flora as compared to those of associated shrubs and herbs. In the present paper we intend to deal with some of these newly discovered small plants (or plant organs) which appear to be of pteridosperm affinity.

As is well known to all paleobotanists, the fragmentary nature of the material preserved in coal balls makes it necessary to describe the isolated plant organs (stems, roots, leaves, fructifications, etc.), with the hope that subsequent work will show their proper assemblage. Thus the seed-ferns as a group were originally described as the Cycadofilicales on the basis of stem anatomy, which seemed to combine both fern and cycad characters along with a constant association with fern-like foliage. It was not until 1905 that seeds were actually found attached to some of these fronds and the present conception of the groups was created. Even now the possession of seeds is definitely known for only the genus *Lyginopteris (Calymmatotheca Hoeninghausi)* and can only be inferred for the numerous other stems which have been carried over into the new classification on the basis of their similar anatomy. Briefly, the characters on which this relationship is based are: small stems, pith or mixed protostele with exarch or mesarch primary wood, secondary wood of characteristic angular (in cross-section) tracheids, reticulate-bordered pitting, usually numerous leaf traces, and an outer cortex containing vertical or horizontal sclerotic bands. Additional similarities and differences are shown in the accompanying table which lists most of the better-known pteridosperm stem genera.

Our new genus (page 289) is validly included through possession of most of the above-listed characters although it lacked leaves and may or may not have had seeds. Its reconstructed habit (plate 5) does, however, show a close flattened branching pattern which offers implications as to the possible megaphyllous development of large fern-like fronds. Such ramification in a single plane, along with the lack of leaves, is suggestive of the Psilophytales, and it is our opinion that *Microspermopteris* may constitute a direct link between that primitive group and the larger seed-ferns. The constant small size (5 mm. or less) of its stems indicates that it would at best have been an inconspicuous element of the forest group and must have been either prostrate or climbing.

The three new species of *Medullosa* described are of course generically identifiable by their polystelic structure as well as by the character of the wood and pitting and, where the latter tissue is preserved, by the fibrous cortex. Here again the evidence of size and form seems to indicate that the habit was either creeping or climbing rather than tree-like.

The two new species of *Dolerotheca* are offered primarily as a supplement to Schopf's (1948) comprehensive work on the genus, although we believe our material does present some basis for additional phylogenetic interpretation as well as possible additional support for the more definite connection of the fructification to the Medullosae.

During the latter course of this study several additional small stems of apparently primitive pteridosperm character have been discovered which we hope to describe in a future paper. One in particular is of interest since, as in *Microspermopteris*, it appears to be leafless. Thus at least a part of the undergrowth of Carboniferous times seems to have occupied a position comparable to that of the living fern allies in that both present a retention of characters primitive for their time so that the excellent fossil record of the coal beds may yet provide the missing links from earlier eras just as those primitive living genera *(Lycopodium, Equisetum* and *Psilotum)* have done in part for the present-day flora.

Microspermopteris aphyllum, gen. et spec. nov.

The following description is based on a total of eight stems occurring in three different coal balls. Four stems were followed through one coal ball for approximately 6 cm. and three stems extended through another ball for approximately 4 cm. The eighth stem was isolated in the third coal ball and was cut as a longitudinal section 1 cm. in length.

All material is from the What Cheer Clay Products Co. coal mine, one-half mile west of What Cheer, Iowa. This horizon lies in the Des Moines series of the Pennsylvanian and is accordingly of Upper Carboniferous age.

The stems followed a relatively straight to slightly sinuous course. Mixed among them were numerous specimens of their smaller, but otherwise identical branches. The stems are of a constant small size even when maturity is indicated by considerable secondary growth. The total diameter including cortex and epidermal tissues never exceeds 5 mm., while the single stele averages 2 to 2½ mm.

The external form of the stems is quite variable, particularly in the smaller specimens where the transverse configuration is almost "amoeboid" in outline (fig. 3). The more mature specimens with considerable secondary growth appear oval to circular in cross-section (figs. 1 and 7).

The primary tissues consist of a protostele in which the large metaxylem tracheids are divided into groups of 12–14 cells by a radiating network of parenchyma, the individual strands of which are usually not more than one cell in thickness and in longitudinal section are seen to be vertically elongated cells, five to six times as long as wide. The inconspicuous protoxylem groups are situated on the periphery of the primary tissue and appear to be exarch though their exact position is vague due to the very small size of the adjacent innermost secondary wood. The metaxylem tracheids increase slightly in size towards the center, averaging 150 μ in diameter as against 50 μ for the secondary wood. All walls of the metaxylem are reticulately bordered pitted with the opposing orifices at a slight angle to one another (fig. 12).

Comparative characters of seed-fern stem genera	Approximate number of steles and stem diameter	Primary wood	Secondary wood and ray structure	Cortex	Leaf traces and petiole	Horizon
Microspermopteris	Single stele Stem: 5 mm.	Exarch; a nearly solid to mixed protostele divided into groups of 12–14 cells by parenchyma network	Secondary wood usually well developed, increasing in size towards outer layers; pitting reticulate-bordered. Rays few, low, uniseriate.	2-zoned; inner zone homogeneous; outer zone with a vertical series of horizontal sclerotic plates	Leaf traces lacking; branch traces concentric and indentical to stele; branching at right angles to stem	Des Moines Series, Pennsylvanian
Lyginopteris	Single stele Stem: 2–4 cm.	Relatively large pith; sclerotic nests with marginal strands of mesarch primary wood	Secondary wood often well developed, interrupted by leaf traces. Rays wedge-shaped, wider towards outside	Inner cortex with sclerotic nests and secretory cells. Outer cortex with anastomosing vertical sclerotic bands; spinous emergences	Leaf traces originate in primary wood on pith margin and pass out through gaps in secondary wood; divide into 2 in cortex and fuse V-shaped in petiole	Carboniferous
Heterangium	Single stele Stem: 1–2 cm.	A mixed protostele, usually mesarch	Secondary wood seldom more than 8–10 layers thick; reticulate-bordered pitting. Rays broad, often wedge-shaped	2-zoned; inner zone with horizontal sclerotic bands; outer zone with vertical sclerotic bands	Leaf traces originate as 1 or 2; always dividing into 4–8 in the petiole	Lower Carboniferous to Permian
Rhetinangium	Single stele Stem: 2 cm.	Exarch; a mixed protostele with very large metaxylem cells and parenchyma with secretory cells	Secondary wood with reticulate-bordered pits on radial walls. Rays broad and high	Inner cortex lacking sclerotic tissue; outer cortex with vertical sclerotic bands	4–5 U-shaped traces with exarch protoxylem form a single corrugated band. Petiole base larger than main stem	Lower Carboniferous
Medullosa	2–8 steles Stems: 2–12 cm. (excl. Permian species)	A mixed protostele with large metaxylem cells. Protoxylem usually exarch	Secondary wood usually with greatest growth towards stem center. Rays thin (1–2 cells) and 1 cm. or more high	Containing numerous collateral leaf traces and resin canals; outer cortex with vertical sclerotic bands	Leaf traces collateral, very numerous. Petioles large with numerous traces	Lower Carboniferous to Permian

Comparative characters of seed-fern stem genera	Approximate number of steles and stem diameter	Primary wood	Secondary wood and ray structure	Cortex	Leaf traces and petiole	Horizon
Sutcliffia	1 large central stele surrounded by small subsidiary strands (meristeles) Stem: 12 cm.	Exarch; a mixed protostele with large metaxylem cells and parenchyma with secretory cells	Secondary wood weakly developed (3–4 rows). Rays thin (1–4 cells), 1–2 cm. high	Outer cortex with vertical sclerotic bands similar to *Medullosa*	Traces concentric, numerous, arising from meristeles. Petioles similar to those of *Medullosa*	Lower Carboniferous
Stenomylon	Single stele Stem: 2 cm.	Triangular mixed protostele; parenchyma bands running from 3 corners to center	Secondary wood well developed; reticulate-bordered pitting on radial walls. Rays broad and wedge-shaped	Inner cortex lacks sclerotic tissue; outer cortex with vertical sclerotic bands	Leaf traces originate from corners of triangular protostele and divide into numerous bundles	Late Devonian and Lower Carboniferous
Calamopitys	Single stele Stem: 2–5 cm.	A pith with endarch primary xylem or a mixed protostele	Secondary wood often well developed (20–30 rows); reticulate-bordered pitting on radial walls. Rays broad	Outer cortex with vertical sclerotic bands similar to *Medullosa*	Leaf traces often concentric, leave stele as 1 or 2 and divide into 6–8 or more in the petiole which resembles that of *Medullosa*	Late Devonian and Carboniferous
Aneurophyton (Eospermopteris) (see footnote, p. 294)	Single stele Stem: 1–2 cm., although 3-ft. stump casts are recorded	Triangular protostele, exarch with protoxylem at the 3 angles	Abundant secondary wood; reticulate-bordered pits on radial and tangential walls. Rays small, thin, 1–2 cells wide	Outer cortex with scattered vertical sclerotic strands	Leaf traces lacking; branch traces similar to main stele but smaller	Middle Devonian
Schopfiastrum	Single stele Stem: 2 cm.	Exarch; a mixed protostele	Secondary wood well developed; reticulate-bordered pits on radial walls. Rays thin and high	Resin canals rare or absent; outer cortex with vertical sclerotic bands	Leaf traces large, bilobed, in opposite pairs	Des Moines Series, Pennsylvanian

The secondary wood ranges from 3–4 rows in thickness in the young small stems to around 16 in the larger more mature specimens. The first-formed cells are quite small, being hardly distinguishable in size from the protoxylem. Their diameter increases gradually towards the outside but never approaches that of the metaxylem. Longitudinal sections of the secondary tissue show the radial walls pitted in the same way as the metaxylem, with a dense reticulum of bordered pits, while the tangential walls have fewer scattered pits, with more lineal openings, arranged in irregular rows up and down the central area. Wood rays are inconspicuous and relatively sparse. They are small, uniseriate and from 1 to 4 cells in height (fig. 9). A rather frequently observed character of the secondary wood of the mature stems is its unequal development (fig. 7) which is possibly due in some cases to differing cambial activity and in others represents the unfilled gaps left by departing branch steles. The tissues immediately surrounding the wood are seldom well preserved and are represented in all of our specimens as merely a thin dark brown ring of crushed cells. There is no evidence of periderm formation.

The cortex is divided into an inner and outer zone of approximately equal thickness. The inner part is composed of poorly preserved isodiametric thin-walled cells containing numerous, scattered dark secretory cells. The outer zone is thicker-walled and usually better preserved, consisting of a compact tissue of brick-like cells (hexagonal to circular in transverse section), about twice as long as wide, the elongation being parallel to the axis of the stem. This merges into an outermost tissue which is 2–3 cells thick and differentiated by being made up of cells four to six times as long as broad. An unusual character of this tissue is the frequent occurrence of multicellular emergences which are commonly broad at the base, tapering to a sharp point. They are sometimes forked and horn-like (figs. 5 and 55) and may occur singly or in clusters (fig. 8). In length they average .6 mm. There is no evidence that they were glandular like the emergences of *Lyginopteris*, nor do they appear to have been arranged in parallel rows as has been described for the latter genus (Scott, 1923). On the contrary, they are produced more or less indiscriminately with the exception that they are nearly always present at the point of departure of a branch.

A feature of the outer cortical zone which is probably the most unique in relation to the comparable pteridosperm genera is the presence of a vertical series of *horizontally* aligned sclerotic plates instead of the usual vertical strands. These consist of thick-walled stone cells, 2–4 cells deep and 4–6 cells in diameter (fig. 10). In tangential section they are occasionally seen to anastomose with adjoining plates at the same level and with plates above and below, thus appearing as a loosely arranged horizontal network (fig. 11).

One of the most difficult problems in interpretation has been the question of whether *Microspermopteris* bore leaves. As stated earlier, we have followed four of the stems for approximately 6 cm., three for 4 cm., and another for about 1 cm.

This produced a close check on nearly 37 cm. of stem, all, of course, not of the same plant. However in this rather respectable amount of material we encountered only five instances of vascular tissue being given off from the main stele. In every case the details are identical and are illustrated for both a young and mature specimen in figs. 1, 2, 3, 5 and 55.

The branch is first evident as a departure from the stele of a complete segment of primary and secondary wood, with the crushed phloem and cambium tissues on its outer, abaxial surface. At this point it consists of 8 to 12 metaxylem cells with possibly 1 to 2 strands of protoxylem, bordered on the outer side by almost the complete amount of secondary wood present at that particular point on the main stele. This results in a conspicuous gap being produced in the mature stems and a relatively smaller one in the young stems where the proportion of secondary growth is much less. The angle of departure is acute (around 30°), the trace following this steep course through the cortex for approximately 2 to 3 mm. During this space the secondary wood and enclosing parenchyma tissues completely surround the primary core and produce a concentric bundle identical to the main stele except in size. The bundle then turns sharply outwards and proceeds at right angles to the stem axis for a distance approximately equal to the normal diameter of the stem before again resuming an upward course. As shown in fig. 5, the branch, where it projects horizontally out from the stem, almost equals the stem in size and exhibits all of its characteristic sclerotic plates and cortical zones. At no time does the bundle show any tendency to subdivide further, while a transverse section of one of the branches at a point around 4 mm. from the main stem shows it initiating a further small branch of its own in the same plane as the primary one. The branching was apparently distichous at relatively long intervals, so that the habit was probably fairly close to the partial reconstruction shown in pl. 5.

Adventitious roots, which are primarily limited to the axis of the branches, are similar to those of *Lyginopteris*. They are commonly hexarch or heptarch with conspicuous protoxylem groups at the points of the projecting arms (fig. 4). The phloem lies between these arms and, as in *Kaloxylon,* there is a small amount of conjunctive parenchyma in the metaxylem. The stele is enclosed by a single poorly preserved dark ring which probably represents the endodermis. The cortex is homogeneous and identical to the inner cortical zone of the stem. The peripheral zone is undifferentiated, so that in transverse section the loosely packed cortical tissue with scattered secretory cells appears to extend clear to the edge of the irregularly lobed outer margin. This lack of a differentiated epidermal zone is one of the distinguishing features between these roots and those of *Lyginopteris*.[1]

Secondary growth is rather rare but when present is again similar to that of *Kaloxylon*, cambial activity initiating in the depressions between the protoxylem

[1] While the information in the literature is often vague on this point, similar roots have also been described for *Heterangium*, although they are usually listed as diarch or triarch (Scott, 1923).

points and producing wedges of typical secondary wood alternating with wedge-shaped rays opposite the protoxylem. The pitting is identical to that of the corresponding tissues in the stem. As might be expected, the roots are of constant small size, with the most mature specimens showing 6–7 layers of secondary growth not exceeding 2 mm. in total diameter. The point of their insertion on the stem offers another similarity to *Kaloxylon* as roots are most frequently found immediately above the branch attachment (see Scott, 1923, p. 49) where their horizontally departing bundle seems to function, in part, in filling up the branch gap. As it has been possible to follow these roots from their insertion on the stem (fig. 6) out to typical transverse sections as in fig. 56, their identity is beyond doubt.

Discussion:

At first glance, in transverse view *Microspermopteris* presents a close resemblance to *Heterangium*. The size is comparable to *H. minimum* (Scott, 1917), and the primary wood with its thin network of parenchyma separating large groups of tracheids is more closely approximated by *H. Kukuki* (Hirmer, 1933) although the total amount of parenchyma is much less in *Microspermopteris*. In the anatomy and insertion of the roots and the presence of multicellular emergences on the stem and branches we have structures comparable to *Lyginopteris*. However, the almost solid protostele contrasts with that of *Lyginopteris*, while the absence of leaf traces and of a vertical fibrous hypoderma, along with the exarch position of the protoxylem, removes all possibility of assigning the specimens to *Heterangium*.

While the horizon of our petrifactions is late Upper Carboniferous and *H. Grievii* Scott is of Lower Carboniferous age, there seems little doubt but that we are dealing with a more primitive plant which possibly represents the ancestral stock of *Heterangium*. In fact, if it were possible to increase slightly the amount of parenchyma in the primary wood, fuse (through webbing) the closely grouped parallel branches into a multi-bundle rachis (Lignier's (1908) theory of megaphyllous development), and add a hypodermal zone of vertically elongated fiber bands we would have a stem quite similar to *Heterangium*. The sclerotic plates lying in the extreme outer cortical zone of *Microspermopteris* (fig. 10) are in radial view somewhat similar to the plates found in the middle cortex of all of the *Heterangium* species (with the exception of *H. minimum* which, according to Scott, lacks fibrous and sclerotic tissue altogether).

The most obviously primitive and unusual feature, the leafless condition, can be assumed to be demonstrated since our material permitted examination of approximately 37 cm. of different stems. The only similar character in plants of possible pteridosperm affinities is in *Eospermopteris (Aneurophyton)* of the middle Devonian.[1] We must assume, then, partly on the lack of any intervening evidence, that we are dealing with a link leading the pteridosperm complex clear back to the

[1] Although the fructifications originally described as seeds were later shown to be sporangia the anatomy of the stem still provides some basis for including the genus in the pteridosperms.

Psilophytales. Indeed, Dawson's restoration of *Psilophyton princeps* (known only from compressions) is disturbingly similar to our own restoration of *Microspermopteris*, particularly in the flattened branching pattern and the presence of spine-like emergences on the stem. Since what we know of *Psilophyton* stelar structure indicates that it possessed only spiral and scalariform pitting there obviously cannot be any direct comparison in internal anatomy with that of the secondary wood and highly developed bordered pitting of *Microspermopteris*. However, the gross appearance is close enough to intimate that a compression form of *M. aphyllum* might be identified as a *Psilophyton*. The middle Devonian genus *Schizopodium* offers a closer parallel in pitting and beginning of secondary growth. However, we consider it here just an example of the early, contemporaneous origin of these characters in contrast to the more conventionally primitive scalariform pits and solitary primary tissues, since the present evidence indicates its relationship to the Cladoxylaceae rather than the Pteridospermae.

In Andrews' (1940) account of the stelar anatomy of the pteridosperms he makes the following observation:

> . . . it should be stated that the view that the pteridosperms represent an intermediate group between the ferns and cycads is no longer tenable. Rather we must look to a common psilophytalean-like ancestor with terminally borne sporangia, a solid protostele and primitive secondary wood for the origin of the ferns and pteridosperms . . .

While we are more inclined to feel that the ferns arose independently, in many ways our present genus fulfils the theoretical requirements outlined.

The possibility that *M. aphyllum* was parasitic and its leafless condition a result of degeneracy rather than primitiveness has not been overlooked. The fact that the habit was probably epiphytic (climbing) or prostrate in a swamp humus tends to lend some weight to such a view as does the apparent absence of stomata and potential photosynthetic tissues. However, since no organs resembling haustoria are present and the roots resemble so closely the aerial ones of *Lyginopteris* we cannot consider a parasitic condition too seriously. At the same time the combination of so many characters common to both *Lyginopteris* and *Heterangium*, along with the more primitive stelar structure and lack of differentiation into rachis and lamina, seems to point rather definitely to an ancestral form from which both genera may have developed independently. This conflicts with Scott's (1923) theory of *Lyginopteris* arising from a developmental series through the subgenus *Lyginangium*, and it may be necessary to reconsider some of Kubart's transitional *Heterangium* species as being actually primitive *Lyginopteris* species leading back to *Microspermopteris*.

Since no seeds or any fertile parts whatever have been found, it is necessary to include *Microspermopteris* among the numerous other organ genera assigned to the seed-ferns on purely anatomical characters. It may be open to question whether in its leafless condition it could have borne seeds. If they were present they were

more than likely terminal on the smallest branch divisions. However, there is no reason for not considering the possibility that the stem anatomy constituting the organ genera of pteridosperms did not precede the development of seeds (i.e. *Eospermopteris (Aneurophyton)*. Certainly in many of the Devonian and Lower Carboniferous Calamopityaceae the presence of seeds is still to be proven, although the degree of differentiation into stem and leaf-bearing organs had obviously reached a more advanced stage than that shown by *Microspermopteris*.

It can be hypothesized that certain small psilophytalian plants struggling for survival in an environment of increasing lushness and density might well have developed a vine-like habit, involving additional conductive stelar tissue as well as supporting sclerotic and fibrous zones, to be followed chronologically by differentiation into leaves (as a more efficient light-catching mechanism) and still later by seeds as a product of the changing and possibly drying environment. Viewing evolutionary change as a response to environmental change, it is difficult to see seed production ever replacing reproduction by spores if there had not been a constant impetus to survival under conditions unfavorable (lack of proper moisture) to spore germination. It also seems likely that the struggle for living space and light preceded the above conditions.

From the original psilophytalian stock larger and anatomically more complex forms would arise independently, leading by gradual ecological adaptations to the recognized groups of Carboniferous plants. Certainly, the contemperaneous association, even as early as the Upper Devonian period, of widely differing stelar structures for the ferns and pteridosperms would seem to indicate that they had a separate individual origin. Some of the earliest known forms assigned to the ferns such as *Arachnoxylon* and *Reimannia* of the Upper-Middle Devonian show definite affinities to the Carboniferous Zygopteroideae, while *Eospermopteris* of about the same age shows many seed-fern characters *in spite of apparently producing only spores*. Thus, although the picture is complicated by the existence of numerous genera from compressions of which we have no knowledge of the internal anatomy (i.e. *Archeopteris*, etc.), the safest and most consistent distinction between the two groups would seem to be stelar structure. Using this as a criterion, it would be possible to have a phylogenetically correct classification including, on the one side, pteridosperms, having only terminal sporangia and, on the other side, ferns exhibiting heterospory. There certainly can be no reasonable objection to recognizing that the seed-ferns must have passed through a sporangiate stage or that ferns may not have achieved heterospory as a terminal development rather than as a stage in seed production.

The designation of the group as Pteridospermae becomes increasingly unfortunate if we recognize their independent origin from the Psilophytales and the fact that the most primitive genera undoubtedly lacked seeds. The same situation has

been dealt with in the Lepidodendrales (i.e. *Lepidocarpon* vs. *Lepidostrobus*) with much less confusion. Here the general plant structure and anatomy have been accepted as the basis for the order, while seed production has been recognized as an advanced stage of heterospory within certain species and genera. For some reason it has never seemed necessary to create the Lycopsidospermae to include *Lepidocarpon* although considered on the same basis as the pteridosperms such should be the case.

The following seem to the author to be the important points to bear in mind in relation to Pteridospermae in question.

(1). They are psilophytalian in origin rather than arising from the ferns.

(2). They are possibly of dual origin, with *Eospermopteris* leading to the Calamopityaceae complex and *Microspermopteris* leading to the *Lyginopteris* and *Medullosa* complex.

(3). Leaves *when present* are large and fern-like; seeds *when present* are basically terminal.

(4). The stem and petiole anatomy is constant and characteristic enough to delimit clearly the group irrespective of known possession of seeds.

(5). Included on the basis of the above anatomical criteria are genera such as *Microspermopteris*, which may or may not have had seeds, and *Eospermopteris*, in which the possession of seeds seems doubtful.

(6). While genera known only from compressions such as *Archeopteris* may be links in the pteridosperm chain, they are just as likely, in the absence of anatomical evidence, to be true ferns. Heterospory, as shown by the modern genera *Salvinia* and *Marsilia*, as well as the fossil lycopods, does not necessarily always imply later seed development.

(7). Seed development in the pteridosperms may in some isolated cases have preceded the differentiation of fern-like leaves with the seeds being borne terminally on naked branches. In other words, we are possibly dealing with early seed-plants which through parallel evolution developed fern-like leaves rather than, as originally thought, with ferns which developed seeds. The distinction may seem trivial, but while the original premises are close the phylogenetic conclusions (depending on which starting point is selected) are quite distinct. The terminal position of the seed in *Lyginopteris oldhamia* and *Aneimites fertilis* are cases in point since these species are among the oldest forms in which seeds are known.[1] (We can only hope that the discovery of fertile material of *Microspermopteris* will illuminate this point.)

Diagnosis:

Stems of constant small size, the stele never exceeding 2.5 mm. or the entire stem 5 mm. *Metaxylem* of large cells (150 μ diameter), diminishing towards the

[1] While these seeds are "terminal" on leafy fronds rather than on naked stems it seems not unlikely that their apical position involves a carry-over from a developmental stage prior to the acquisition of leaves.

periphery. Protoxylem exarch, of numerous indistinct groups. Xylem parenchyma arranged in a thin network enclosing groups of 12 to 14 metaxylem cells. *Secondary wood* of small angular (in cross-section) tracheids from 3 to 16 layers in thickness, increasing in size towards the outer edge. Reticulate-bordered pitting with crossed orifices in the metaxylem and on radial walls of the secondary wood. Scattered bordered pits with lineal openings on tangential walls. Protoxylem spiral or annular. Rays rare or lacking; when present, small, uniseriate, 1–4 cells high. *Cortex* differentiated into inner and outer zones. The inner zone composed of isodiametric thin-walled cells, poorly preserved, with scattered secretory cells but lacking sclerotic tissue. Outer zone of thicker-walled, longer cells containing vertical series of horizontal sclerotic plates. *Epidermis* of similar but more elongated cells producing numerous multicellular pointed emergences. *Leaf traces* lacking. Branching distichous and at right angles to the stem. *Roots* adventitious, hexarch to heptarch, commonly inserted above point of branch departure.

Horizon: Des Moines Series of Pennsylvanian.

Type: fig. 1. Slide 1602 in the paleobotanical collection of the Henry Shaw School of Botany of Washington University.

SOME NEW AMERICAN MEDULLOSAS

In the interval since Thiessen (1920a, 1920b) discovered and identified a pteridosperm stem as *M. anglica* (later to be assigned varietal distinction by Schopf, 1939) three new species and one variety of *Medullosa* from American coal balls have been brought to light. They are: *M. Noei* (Steidtmann, 1937), *M. distelica* (Schopf, 1939), *M. Thompsonii* (Andrews, 1945), and *M. anglica* var. *ioensis* (Andrews & Kernen, 1946). With the exception of *M. Noei* all of these new species and varieties have formed a fairly closely integrated group assignable to the subgenus Anglorota along with the European species *M. anglica, M. centrofilis,* and *M. pusilla. M. Noei,* showing affinities with *M. Leuckarti,* is held to be transitional between the Carboniferous form cycle and the Permian species.

Our knowledge of this very interesting group has been expanding rather rapidly, and with the hope of throwing still further light on the subject three new species of *Medullosa* are herewith described and additional new data are presented on *M. Noei.*

Medullosa primaeva, sp. nov.:

The following description is based on a single coal ball specimen from the Urbandale Mine located 1.2 miles west of Des Moines, Iowa, on U. S. Highway No. 6. This is the same location from which Andrews (1945) described *M. Thompsonii.* The horizon is the Des Moines Series of the Pennsylvanian. The material was collected and cut by Mr. Frederick O. Thompson of Des Moines, who generously donated it to the Henry Shaw School of Botany of Washington University. It consists of a cut block 5.5 x 5.5 cm. and 1.3 cm. thick, with the stem

exposed on one side through a fracturing away of the adjoining material. The stem's course is through the thickness of the block at a slight angle from the vertical, the total available length being 1.4 cm. Figures 14 and 15 show the appearance of the top and bottom surfaces of the specimen prior to any grinding of the fractured edge. Approximately one half of the cortex and external tissues have been lost on the side of the fracture, though the multiple stele appears to be nearly intact.

As shown in fig. 14, the upper[1] surface of M. *primaeva* exhibits 5 rather large and uniform-sized steles, 2 of them partially fused. There are also 2 small steles and a portion of a third on the fractured margin. The lower surface shows the same 8 steles, though somewhat altered in orientation and size, with 3 of the steles partially fused. It is not implied, however, that 8 was the constant number of steles as even in the short length of stem available stelar fusions and divisions were numerous and the diversity of vascular growth even included the production of steles running horizontally through the stem for short distances (fig. 13). Still, even with these variations the stele number seems to have been constantly 6 or more.

The stem measures 2.0 cm. in diameter, the individual steles ranging from around 5 mm. for the average large ones to .5 mm. for the very smallest. The 5 largest steles are closely comparable in size to those of M. *Thompsonii* even though the stem of the latter is considerably larger, averaging 3.5 cm. in diameter. The steles are essentially radially symmetrical with a very slight tendency towards endocentricity.

It may be argued that some of the smaller vascular strands (fig. 14, S3 and S8) do not constitute true steles. However, even the smallest possesses 8 or more layers of secondary wood and can be seen to be independent in its course throughout the entire length of the specimen (fig. 13). Neither can they be designated as accessory strands from which leaf traces might be produced (as in *Sutcliffia* and M. *anglica*) since the two largest of the 8 steles are, in our specimens, the sole observed source of trace departure.

The primary wood is small in amount and is characterized by the almost complete absence of parenchyma; what little there is being restricted to a thin network running through or enclosing the primary cylinder, from which the high uniseriate rays extend out through the secondary wood. The primary wood forms a cylindrical to irregularly shaped core around which it is often difficult to determine the exact inner limits of secondary growth. The protoxylem is not distinguishable (figs. 14 and 19).

The secondary wood is variable as to cell size and radial growth, the first-formed layers being often composed of large tracheids (similar in size to the metaxylem) which merge some distance out into rows of much smaller cells. On

[1]The interpretation as to lower and upper surfaces of the stem is made on the basis of the outward passage of leaf traces exposed in a series of longitudinal peels.

the other hand, the same stele may, on the opposite side, show the first-formed secondary wood to consist of very small (in diameter) tracheids and the successive outermost cells to be large (fig. 19).

Each stele is enclosed by a dark tissue of crushed cells, probably of cambium and phloem, in which are occasional small resin canals. The entire stelar assembly is surrounded by a very thin, parenchymatous "periderm" which is never over 2 to 3 cells thick and is often so poorly preserved as to be indistinguishable from the cortex.

The rays are up to 1 cm. or more in height and apparently constantly uniseriate. In this regard they probably come closest to Andrews' (1940) classification II B in which he originally placed all of the Anglorota group as well as *M. Noei* and *M. Leuckarti*.

The cortex is composed of cells rounded in transverse view but elongated vertically two to three times their width. Traversing upward and outward through the cortex are numerous small collateral leaf traces consisting solely of 3–4 protoxylem tracheids with spiral thickening (fig. 27) and an abaxial phloem group. There is definitely no secondary wood associated with the trace. Mucilage canals with their "resin rodlets" are scattered sparingly through the cortex and are unusually small, having a constant diameter of less than 60 μ. They are commonly closely associated with the leaf traces and, in contrast to the majority of the other American species, seem to have seldom invaded the hypodermal, sclerotic strand zone.

The sclerotic strands form a single layer and in transverse view appear circular to slightly radially elongated. They are separated by 2–3 layers of cortical-like cells from a conspicuously darkened epidermis. This latter tissue consists of brick-shaped cells with a slight tangental elongation and rather thick walls which occasionally show evidences of a cuticle.

Discussion:

Our specimen shows a rather close similarity to *Medullosa Thompsonii* in the secretory canals—their small size, their comparative scarcity in the stem as a whole, and their almost complete absence in the sclerotic fibrous zone. However, although Andrews (1945) points out that the number of steles in the Medullosae is generally an unreliable taxonomic character (stelar divisions and fusions often resulting in variations of 2–3 or more steles), the possession by *Medullosa primaeva* of 7 to 8 steles, which tend to pursue horizontal courses through the stem and almost completely lack conjunctive primary parenchyma, clearly makes it of specific importance and distinct from M. *Thompsonii*.

Medullosa centrofilis and M. *pusilla* are the only other species which seem similar enough to deserve consideration. The former comes closest to M. *primaeva* in number of steles (considering the "star ring" as a fourth stele) but lacks the horizontal stelar meanderings and exhibits many more and larger secretory canals. M.

pusilla is comparable in over-all stem size but again is separated by the stele number, the difference between 3 and 7–8 being held as more than specific variation.

The slight tendency toward endocentricity of the secondary wood and paucity of conjunctive parenchyma in the primary area, along with its generally netted arrangement, make the individual steles more closely comparable to those of *Microspermopteris* than to *Heterangium*. According to Bower's (1930) "size and form" principles one would expect relatively little parenchyma in steles of such small size, but comparison with the equally small stele of *M. Thompsonii* seems to show greater differences than can be accounted for on the basis of Bower's hypothesis. Thus although the *M. primaeva* stelar number is much larger than in any of the other species of equivalent age the general stele structure appears to be more primitive. This is in contrast to what might be considered advanced development as evidenced by the absence of secondary wood in the leaf traces and leads one to believe that the presence of such secondary wood in *M. anglica* is not necessarily indicative of a primitiveness either for the character or the species as a whole. On the contrary, it seems most logical at present to consider *M. primaeva* with its numerous small, radially symmetrical steles as having developed from a monostelic stem through stelar proliferation and accordingly representing a primitive stage of the genus.

The specific name *primaeva* has therefore been assigned.

Diagnosis:

Stem small, not exceeding 3 cm. Steles numerous, 6–8, frequently fusing and dividing, ranging from .5 to 5 mm. in diameter, often pursuing a sinuous horizontal course through the stem. Primary wood parenchyma small in amount or lacking. Resin canals small and few, almost entirely absent from fibrous hypodermal zone. Rays uniseriate; secondary wood of variable cell size; irregular radial growth, only slightly endocentric.

Horizon: Des Moines Series, Pennsylvanian.

Type: Fig. 14. Slide 1615 in the paleobotanical collections of the Henry Shaw School of Botany of Washington University.

Medullosa elongata, sp. nov.

The following description is also based on coal-ball material collected by Mr. F. O. Thompson and his associates of Des Moines, Iowa. The source was a large open pit mine of the Atlas Coal Co. located in Wilson County, Iowa. The horizon is Pennsylvanian, Des Moines Series.

The greater part of material from this locality was too heavily pyritized to permit good plant preservation, but the stem fragments which were identifiable indicate a flora consisting primarily of *Lepidodendron* and *Calamites*. Pteridosperms were relatively rare, the present description being based on a single stem specimen 7 cm. long and 6 x 1.5 cm. in diameter. There evidently had been some crushing, which would account partially, but not altogether, for the asymmetry (fig. 16).

The outstanding feature of the three steles is their extreme endocentricity in which character they resemble Schopf's (1939) *M. distelica.* The steles maintain their individuality, i.e., no stelar fusion, and relative position throughout the 7 cm. of stem length with the endocentric secondary development also showing a constant approximate 4 to 1 ratio in thickness as compared to the exocentric secondary tissues. The three steles are of equal size, averaging 10 × 2 mm., the plane of elongation following that of the stem as a whole and constituting a factor in the evidence that the general asymmetry was a natural character of the living plant. Two of the steles occupy a position directly opposite one another and near the center of the stem while the third is isolated off to one side (fig. 17). The primary xylem consists of a long narrow area following the elongation of the stele. It is seldom over 2 cells in width and runs up to 8 mm. in length. The metaxylem tracheids are large (.2 mm.), and usually triangular in cross-section. There is relatively little conjunctive parenchyma, while the protoxylem is indiscernible.

The secondary wood is rather unusual for a *Medullosa* in that the majority of the cells are square in transverse view, while the others are of the more characteristic alternately arranged pentagonal shape. Also, in contrast to the somewhat similar *M. distelica,* the radial rows of secondary tracheids are not conspicuously divided by rays nor are the outermost cells differentiated. In addition, the rays are uniseriate, not particularly numerous, and almost impossible to detect in transverse view.

Surrounding each stele is a thin dark layer of crushed cells containing numerous small resin canals. The periderm is thin (3–4 cells), poorly preserved, and apparently interrupted at the narrow ends of the steles where the leaf traces are given off. The cortex is rather poorly preserved due to pyritization, with numerous rather large slime canals (.2 mm. in diameter) scattered throughout it and also conspicuously associated with the fiber strands in the sclerotic-fiber hypodermal zone. The fiber strands are arranged in 2–3 alternating rows, the individual strands being somewhat radially elongated. A rather striking character of the species is the large "compound" resin canals running horizontally through the stem. They measure 1.3 mm. in diameter and are approximately six times the size of the vertical canals. Figure 18 illustrates several of these canals at the same magnification as the vertical canals in fig. 17. They are lined with numerous small triangular and diamond-shaped secretory cells which appear to contain the same black resin substance as the canal itself.

The leaf traces are given off from the narrow ends of the flattened steles and are initially quite large, consisting of 10–12 or more primary tracheids which divide farther out in the leaf bases into numerous smaller bundles. Three leaf bases are shown in fig. 16, two detaching themselves from the narrow transverse extremities of the stem and approximately parallel to it, while the third is being given off from the stem's broad side and at right angles to it. Thus it would appear that in *M. elongata* we are dealing with a creeping stem of possibly dorsi-

ventral symmetry. As stated earlier, the dimensions of 6 × 1.5 cm. for the stem can be only slightly attributable to crushing while the equivalent asymmetry of the steles and general lack of any crushed tissue indicate the form to be more or less characteristic of the living plant. In addition, the 7 cm. of stem length of our specimen exhibits rather short internodes, with several leaf bases given off in the same bilateral plane from the narrow opposite stem sides.

The position of the stem on the edge of the containing coal ball prevented observation of more than the one dorsal leaf base shown in fig. 16. However, it seems plausible that these erect leaves were produced between internodes as short as the lateral ones.

As implied previously, *M. elongata* is most closely comparable to *M. distelica* on the basis of the extreme endocentric secondary growth. However, in the possession of three steles, which at no time show any tendency towards fusion, the difference in primary wood, fewer and uniseriate rays, and square secondary tracheids, as well as the large compound resin canals and apparent dorsi-ventral habit, *M. elongata* is clearly distinct and of specific importance.

The species name *elongata* is assigned in recognition of the asymmetric transverse elongation of the steles (10 × 2 mm.), as well as the equivalent transverse elongation of the stem as a whole.

Diagnosis:

Stem asymmetric to bilaterally symmetric, approximately 6 × 1.5 cm. in diameter, only slightly crushed in the smaller dimensions. Steles 3, extremely endocentric, 2 opposite one another in stem center, the third isolated to one side, retaining their relative positions and not fusing or dividing in over 7 cm. of stem length. Vertical resin canals numerous, averaging .2 cm. in diameter; fewer horizontal, large compound resin canals averaging 1.3 cm. in diameter. Habit creeping or climbing with leaves being given off from sides and dorsal surface of stem.

Locality: Atlas strip mine, Wilson County, Iowa.

Horizon: Pennsylvanian, Des Moines Series.

Type Specimen: Fig. 16. Slide 1617, in the paleobotanical collections of the Henry Shaw School of Botany of Washington University.

Medullosa endocentrica, sp. nov.:

This third new medullosan stem comes from coal-ball material found in a stream bed outcropping near Berryville, Illinois. The location is near to that from which Steidtmann (1937) described *M. Noei,* and the horizon is the same, being determined as the upper part of the McLeansboro group of the Pennsylvanian of Illinois. The coal ball containing the specimen was 15 cm. long by 8 cm. wide. The stem followed a straight course through almost the complete longer axis, being itself 12 cm. long and 1.2 × .7 cm. in diameter. These dimensions are of the stelar system only, the cortex and other external tissues having been lost. However, as can be seen by referring to fig. 20, the unique appearance of the steles seems

to justify recognizing the specimen as a new species and possible culmination of endocentric development, in spite of the lack of information as to the stem's external anatomy.

The stem consists of 3 steles, 2 of which are 5 × 5 mm. in diameter, the third, 2 × 1.5 mm. in diameter, situated on the side equidistant between them. Secondary growth is almost entirely endocentric, only one of the larger steles showing a very small amount of exocentric growth. These characters are constant for the entire 12 cm. of stem length as are also the relative stelar positions. Thus there can be little doubt that this extreme centripetal growth was a distinct feature of the living plant, and the evidence also suggests that the stelar system had achieved a degree of uniformity not found in any of the other Anglorota species.

The primary area of each stele is oval in transverse view, and measures 1.5 × 1 mm. in the 2 larger steles. It consists of scattered groups of large metaxylem cells intermixed with considerable conjunctive parenchyma. The protoxylem appears to consist of two small exarch groups of tracheids with annular thickening while the metaxylem shows the characteristic dense reticulate bordered pitting.

The secondary growth is produced in a fan-like pattern, radiating towards the stem center for an average of 15 cells in the large steles and 6 cells in the small stele. The transverse dimension of the cells increases gradually from the innermost to the outer rows but on the average is quite large, around .2 mm. The rays are of great height, more than 1.7 cm., and in the wood are uniseriate or at the most 2 cells wide. They commonly separate radial rows of 2–3 tracheids (fig. 22).

The pitting of the secondary wood is bordered and densely reticulate on the radial and oblique-tangential walls, with relatively few scattered pits on the directly tangential surfaces. The length of the individual tracheids is also quite extreme, an almost perfect tangential section showing them to be over 1.7 cm. Adjoining the outermost secondary wood (and continuous with it in general pattern and ray position) is a rather disorganized tissue which we were at first inclined to interpret as undifferentiated secondary wood. It consists of large thin-walled cells, similar in size and shape to the secondary tracheids but completely unpitted. On entering this zone the thin rays of the wood become greatly expanded, averaging from 4 to 8 or more cells in width, and appearing to be completely mature in their development (fig. 21). This point, along with the total absence of any rudimentary pitting, in either the tangential or radial walls of the vertical elements, in our opinion, makes it very unlikely that the cells are immature secondary tracheids. On the other hand, one or two of our tangential peels through this zone shows vestiges of what appear to be disarranged transverse walls with extremely small pores similar to the sieve plates of living plants (fig. 23). Scott, in his description of *M. anglica,* has pointed out that the rays become much wider in the phloem zone, while exceptionally large sieve tubes are common to plants of vine-like habit. Therefore, on the basis of the above evidence (which may be not entirely conclusive), along with the position of the tissue, we are inclined to consider it tentatively as phloem-like in nature.

Lying between this phloem region of the three steles is a thin parenchymatous zone of vertically elongated cells in which are scattered numerous resin canals containing their opaque resin rodlets. The entire stelar assembly is completely surrounded by a thin layer of dark, crushed cells of possible periderm nature.

The specific name *endocentrica* is assigned on the basis of the complete and constant centripetal secondary growth.

Diagnosis:

Steles small, not exceeding 5 × 5 mm., 2 opposite one another and of equal size, the third smaller, situated on the side between them. Secondary growth completely centripetal. Primary xylem exarch. Metaxylem with considerable conjunctive parenchyma. Rays 1–2 cells wide, expanding in the conspicuous phloem zone to 4–8 cells in width, exceeding 1.5 cm. in height.

Horizon: Upper part of the McLeansboro group, Pennsylvanian of Illinois.

Type: Fig. 20. Slide 1619 in the paleobotanical collections of the Henry Shaw School of Botany of Washington University.

Discussion:

As stated previously, *Medullosa endocentrica* appears to represent the ultimate in centripetal secondary development, and accordingly its closest affinities lie in the direction of *M. distelica* and *M. elongata.* It differs from the former primarily in possessing a third distinct small stele, constant for the whole stem and in the more perfect symmetry of the opposing "twin" steles. It differs from *M. elongata* in stele shape (*M. elongata* averaging 10 × 2 mm.), as well as in the character of the primary wood and amount of conjunctive parenchyma. *M. endocentrica* differs from all the other Medullosas in its constant degree of endocentricity and the possession of a unique phloem zone of exceptionally large sieve tubes.

It is possibly significant that here, as in *M. elongata,* we appear to be dealing with a stem of more bilateral (dorsi-ventral) than radial symmetry. From the form of stele development in *M. endocentrica* (fig. 20) leaf traces could only have been given off in the three planes opposite the abaxial sides of the primary xylem groups. Thus while the orientation of the steles is somewhat different in the two species it is likely that the phyllotaxy was similar, the leaves being produced laterally and vertically (dorsally) with the side lacking a leaf trace source being considered ventral.[1] The predominance of 3 stele forms in the Medullosae is perhaps indicative of this trend, which, however, reaches its inescapable climax only in the extremely endocentric species. *M. endocentrica* has apparently almost reached the limit of its potential stem enlargement through secondary growth but it is still much too small to permit interpretation as an arborescent plant. Therefore it could not possibly

[1] It should be pointed out here that since the traces show no evidence of "girdling," the direction of their initial departure is a valid indication of the stem's phyllotaxy.

have attained a habit comparable to that suggested in the reconstruction of M. *Thompsonii* (Andrews, 1945). Also if it produced relatively large *Alethopteris*-type fronds, as appears likely from the numerous associated leaves, it must have been a prostrate or climbing vine since the small stem would be incapable of supporting any such great weight. Thus the line of endocentric development from M. *distelica* and M. *elongata* to M. *endocentrica* appears to be one leading to constantly diminishing size accompanied by a change from radial symmetry of the stem with complete spiral phyllotaxy to a bilateral, dorsiventral symmetry with lateral and dorsal leaves. Extreme asymmetry can accordingly be seen to be an advanced rather than primitive character, which as it reached its climax resulted in a line of "dead-end" development in which the stem size was small and fixed. In this viewpoint we agree with Schopf (1939, page 204) where he states:

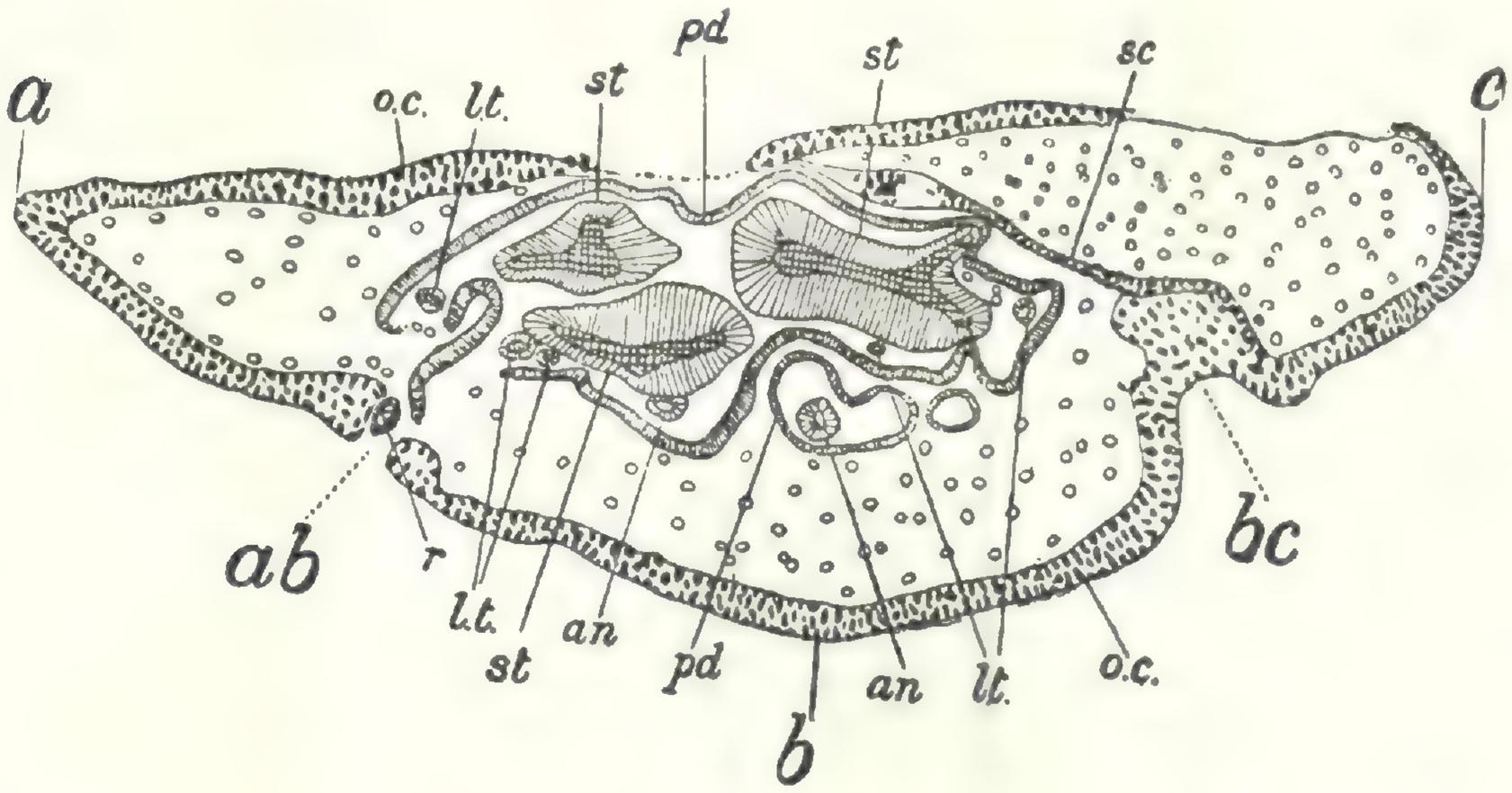
> It seems more tenable to consider the distelar condition in the new Nashville *Medullosa* as reduced from a more polystelar type rather than as directly derived from an ancestry reminiscent of *Sutcliffia*. It is also apparent that the extreme endocentric asymmetry found in M. *distelica* is not a primitive feature.

We have included in the above quotation Dr. Schopf's statement on a distelar condition probably resulting from the fusion of a polystelar type in that it also agrees with our conception of what seems to be another and more important line of development in the Medullosas. As pointed out in the discussion of M. *primaeva*, a polystelar condition with numerous small radially symmetrical steles would seem to have arisen most logically by stelar proliferation of a monostelic stem with a similar small symmetrical stele. Then through subsequent tendencies to stelar fusion the line would lead through the small tetra- and tri-stelar forms to the large asymmetric stelar forms such as M. *anglica* and M. *Noei*.

The fact that the smallest species (M. *primaeva* and M. *pusilla*) have the most radially symmetrical steles while the larger species (M. *Thompsonii*, M. *elongata*, M. *distelica* and M. *anglica*) all have greatly elongated (transversely) asymmetric steles is evidence, in our opinion, that the latter have been derived from polystelic fusion. (A good example of this point is illustrated in Andrews' (1945) diagrams of stelar fusion in M. *Thompsonii* where it can be seen that the fusion produces a larger, more asymmetric and more endocentric stele). Where the fusion standardized itself at 3 steles of approximately equal size, or with one slightly smaller, a balance appears to have been reached which was only upset by the origin of the erratic cambial growths of M. *Noei*.

Regarding the phyllotaxy of the predominately 3-steled forms it may also be pointed out that while the leaf arrangement has been mainly interpreted as spiral, Scott, in working with a specimen of M. *anglica* one foot in length, showed that the leaves were still produced on only three sides of the stem (text-fig. 1). While Scott himself did not enlarge on this evidence, it seems to imply (when correlated with forms such as M. *elongata* and M. *endocentrica*) that the significance of the normal number of 3 steles in the Carboniferous Medullosas lies in the essentially

dorsi-ventral habit of the plant as a whole. As may be noted in text-fig. 1 of *M. anglica* (which is typical for most of the 3-stele species), the steles are arranged in the shape of a flattened triangle, the obtuse apex being always towards the flattened side of the stem from which the dorsal leaf bases are produced, while the steles at the opposite acute angles are oriented towards the position of the lateral leaves.



Text-fig. 1. *Medullosa anglica: o.c.*, outer cortex; *l.t.*, leaf trace; *st*, stele; *pd*, periderm; *sc*, sclerotic strands separating petiole from stem; *r*, root; *an*, accessory strand. *A*, *B*, *C*, *AB* and *BC* represent the points of leaf departure with the phyllotaxy being 2/5. *Note that this arrangement still leaves one side of the stem completely devoid of leaves; so that the habit may be assumed to have been dorsi-ventral* (after Scott).

This bilateral symmetry is borne out also in the over-all stem shape of nearly all of the 3- to 4-steled group. *M. centrofilis* had a stem diameter of 5 × 1.5 cm.; *M. pusilla*, 2.2 × 1.3 cm. (Scott points out that the larger diameter here had lost considerable tissue and was probably still greater in life); *M. Thompsonii*, 7 × 2.5 cm.; *M. anglica*, 10.5 × 3.7 cm.; *M. elongata*, 6 × 1.5 cm. *M. endocentrica* also undoubtedly had a flattened stem but the lack of preservation of the outer tissues in our specimen precludes such measurements. All of the above figures include the attached leaf bases, but since it has been shown that these were always decurrent for long distances on the stem and more or less overlapped, the measurements give a truer habit proportion than those of the stem alone would. The asymmetry can be seen to be quite constant in a proportion of 3:1, which fact alone makes it extremely doubtful that it is altogether due to crushing. De Fraine states for *M. centrofilis* that "the shape of the stem with its covering of leaf bases was thus distinctly flattened."

It would seem that the dorsi-ventral habit, while most obvious in species such as *M. elongata* and *M. endocentrica* was also the rule in the majority of the other species. *M. Thompsonii* is a possible exception since rather careful study of the type specimen seems to indicate that in this particular stem the orientation of the stelar assembly tends to vary, so that the planes of leaf trace departure are dis-

tributed more generally in the four opposing radii and thus supply petioles in a true radially symmetrical spiral phyllotaxy. However, such variations are not too unusual. *Selaginella,* for example, in the two present-day species, S. *rupestris* and S. *apoda,* shows a variation from erect plants with radial symmetry to creeping plants with bilateral symmetry. This view, accordingly, makes it necessary to visualize the Medullosae as primarily an assemblage of creeping or climbing plants rather than as comparable to present-day tree ferns. The prostrate habit has previously been postulated by several earlier workers on the basis of the small stem of the Anglorota plants, while the great stem length recorded by Weber and Sterzel (1896) for some of the Permian specimens is almost conclusive proof of the vine-like habit of the much younger species. Weber and Sterzel state:

> Bei Stämmchen wie M 43, das bei 92 cm. Länge nur einen Durchmesser von durchschnittlich 8,8:4.4 cm. besitzt, könnte man wohl an die von Göppert & Stenzel vermutete Schlingpflanzennatur der Medullosen denken. . . . Die im Anhang sub 1 Seite 105 (64) geschilderten Medullosenstämmchen beweisen dass insbesondere *Medullosa stellata* einé schlank-cylindrische Gestalt mit periodischen Anschwellungen des Holzkörpers und auch im Uebrigen merklich wechselndem Durchmesser haben könnte, so das man, wie schon erwähnt, mit Göppert & Stenzel an Schlingpflanzen denken könnte. In dieser Form des Wachstums liegt wohl auch das verhaltnismässig häufige Vorkommen von Bruchstücken dieser Art begründet.

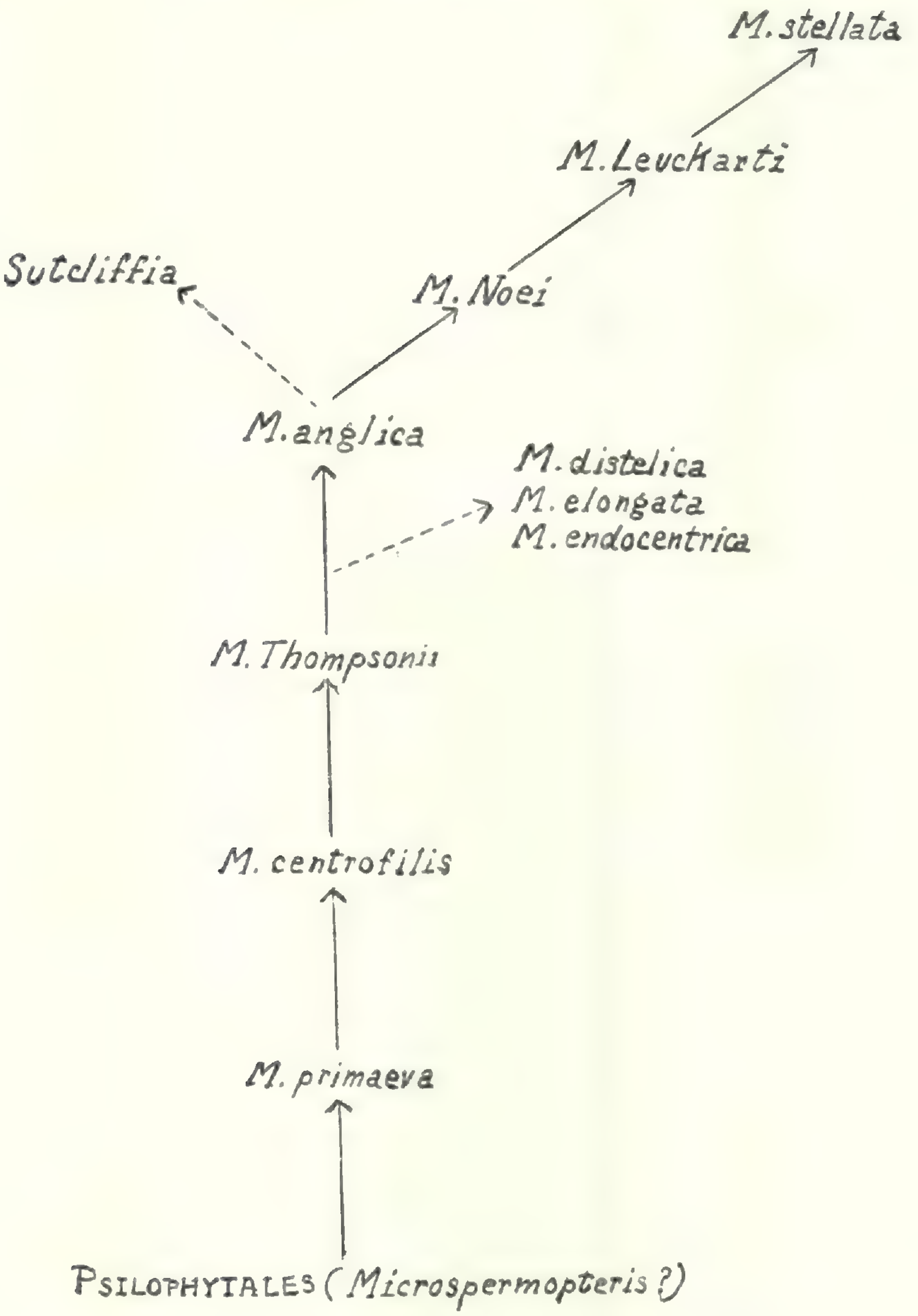
In addition to the evidence offered by the dorsi-ventral flattened stem, the phyllotaxy, and the great stem length in relation to its width, there is also considerable anatomical proof that the Medullosae were primarily prostrate or climbing vines. Solereder (1908) has shown that unequal xylem growth and flattened stems are characteristic of many living lianas, while Westermaier and Ambronn (1881) have pointed out that tracheids and sieve tubes of more than average diameter are typical of living climbing plants. As noted by Andrews (1940), the tracheids of M. *Noei* and M. *anglica* may reach a diameter of 250 μ (larger than most vessels) while M. *endocentrica* has extremely broad sieve tubes.

Although the acquisition of concentric rings of exocentric secondary wood permitted an increase in size of the Permian Medullosas, along with a possible return to a radially symmetrical spiral phyllotaxy, the vine-like habit of their Carboniferous predecessors appears to have been largely retained.

The absence of a vine-like habit in the living or fossil cycads need not present any insurmountable difficulties in retaining the theories of their origin from the Medullosas, since, with the increased girth afforded by centrifugal secondary growth, the developmental trend may be assumed to have been away from climbing towards arborescent forms. This change may also have been influenced and accompanied by a disappearance from the scene of the potentially supporting *Psaronius, Calamites* and *Lepidodendron* through a gradual shift to a xerophytic environment.

To summarize and restate our evidence:

1. A large number of small symmetrical steles with almost solid primary wood represents the primitive condition. Of the different specimens which have so far



Text-fig. 2. Proposed *Medullosa* phyletic chart. Explanation in text.

been described, *M. primaeva* seems to most nearly represent this stage. In this light it seems probable that the origin was not from *Heterangium* but rather from a more ancient form possibly akin to *Microspermopteris*. Arnold (1940) has described a small polystelic stem from the Middle Devonian of New York to which he has given the name *Xenocladia medullosina*. It consists of 9–10 small (not much over 1 mm.) steles with a small solid protostele. He states that: "*Xenocladia* may eventually prove to be a representative of some intermediate stage between the Psilophytales and certain of the polystelic Pteridosperms." While we

are not inclined to attach too much weight to any direct connection between *Xenocladia* and a stem such as *M. primaeva*, it does show the possible origin of a polystelic structure contemporaneous with *Rhynia* and *Hornea* and, along with *Microspermopteris*, indicates a psilophytalian origin for the pteridosperms.

2. Through subsequent tendencies to fusion the stele number eventually became standardized at 3, with occasional variations of 2 or 4 through further fusion or division.

3. Accompanying the above transition there was an increase in the size of the plants and consequently of the leaves, which (since in a closely grouped polystele the leaf traces of necessity are produced from the abaxial sides) tended to inhibit exocentric (centrifugal) secondary growth and thus resulted in an endocentric (centripetal) asymmetry of the steles.

4. As this endocentricity became pronounced the production of leaf traces also became more localized on the abaxial stelar sides, resulting in a phyllotaxy of lateral and dorsal leaves (text-fig. 1, *M. anglica*). *M. elongata* and *M. endocentrica* represent a climax of this trend which in the latter undoubtedly formed an end development.

5. Where the endocentricity did not reach such extremes, the plants tended to increase in size through the production of accessory vascular strands *(M. anglica)*, while eventually tangential secondary growth (to compensate for the limitations of endocentric growth), along with the origin of prolific erratic cambial zones *(M. Noei)*, led to the larger and more complex Permian species. Text-fig. 2 shows a provisional and tentative phyletic chart based on the above points. Although the horizon of all of the American species is considerably higher than that of the European ones, the evidence of the stems themselves still seems to justify the reverse grouping. For the reasons given above *M. primaeva* constitutes the base with the main line of development leading through *M. Noei* and *M. Leuckarti* to the Permian forms, while the three extremely endocentric species constitute a dead-end side chain of development.

Medullosa anglica is placed near the top because of its relatively large size and erratic "periderm" resembling that of *M. Noei*. The large leaf traces with secondary growth may be viewed as advanced and of the nature of specialized accessory vascular strands to supply the increased needs of the enlarged petioles. Also *Sutcliffia*, differing from *M. anglica* primarily only in its monostelic structure, may be regarded as resulting from a fusion of the three steles.

Medullosa Noei Steidtmann:

Steidtmann (1937, 1944) established *M. Noei* as the first clearly recognizable American species of the genus and gave us an excellent description of the salient features and peculiarities of the stem as well as the associated leaves, roots, and seeds. However, the holotype on which he based most of his description had only

one stele with portions of two others, while our present specimen consists of a nearly entire stem with three large complete steles. It was collected from the same outcrop near Berryville, Illinois, that produced *M. endocentrica* and is exceptionally well preserved in its cellular details. The coal ball, of which the stem constituted almost the entire bulk, was 28.6 cm. long and approximately 16 × 7 cm. wide in the middle portion, tapering to blunt points at either end.

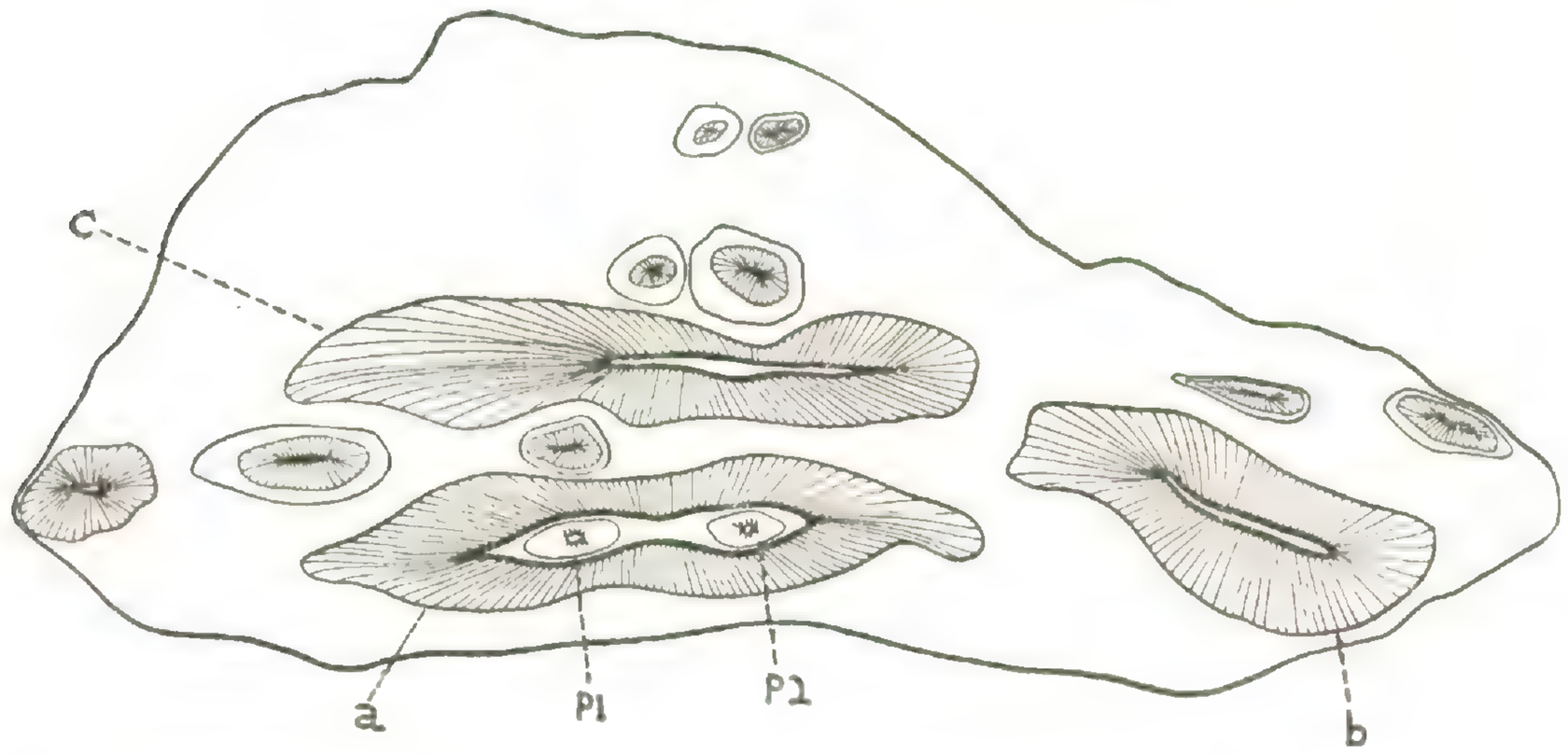
The essential features offering possibilities of an enlarged interpretation and understanding of the species are:

1. The presence of a distinctive phloem zone characterized by broadened extensions of the medullary rays.

2. "Periderm rings" which show a transitional development of secondary wood, a stelar origin, and a remarkable similarity to the Permian Medullosae "star-rings."

3. Adventious roots, which run for long distances through the cortex parallel to the steles, range from triarch to pentarch, and show a well-preserved aerenchymatous cortex.

Before discussing these points in detail a brief description of the stem as a whole will be given. As shown in text-fig. 3, there are three large steles, tangentially elongated, which occupy the major portion of the area as seen in transverse section. Throughout the 28.6 cm. of stem length they remain essentially independent although steles *a* and *c* occasionally partially fuse and then re-separate. Their orientation with relation to one another is similar to that of the steles in *M. elongata,* two of the steles being side by side while the third occupies a position off to one side. They average 6 × 1.5 cm. in diameter and show no particular endocentricity, the secondary growth being the greatest in a tangential plane rather than towards the stem center. This is a greater elongation than was usual in Steidtmann's specimen, although he records that the stele did at times reach a measurement of 6 × 1.8 cm., which is certainly close to the above. For the rest, the primary and secondary wood are essentially equivalent to Steidtmann's specimen and exhibit primary tracheal bundles, prolific and erratic "periderm" growths, and tetrarch roots originating in and running through the primary area. The cortex is crowded with "periderm" rings and tangentially elongated bands, as well as with the numerous large adventitious roots with their many small branches. The hypodermal sclerotic zone is present as the outermost limiting tissue, the leaf bases being absent. While there are apparent general differences between the present specimen and Steidtmann's diagnosis of *M. Noei* (mainly in the lack of any pronounced endocentric growth, and absence of a definite broad periderm zone), it is felt that the variations fall within those allowable to a species, particularly in the Medullosas. The following descriptions of the previously outlined characters are therefore intended solely as an addition to the *M. Noei* diagnosis and not as of new specific or varietal importance.



Text-fig. 3. *Medullosa Noei: a, b,* and *c* indicate the three steles. *P1* and *P2* are the "periderm" or "cambial" rings. All of the other vascular strands represent adventitious cortical roots. Additional explanation in the text. × 4/5.

It is understandable how a great deal of the *M. Noei* material might be examined without observing the striking phloem rays, since they are only occasionally evident even in the exceptionally well-preserved present specimen, their place being usually occupied by invasions of the prolific "periderm" tissue. However, as shown in fig. 26 the rays with their dark brown secretory cells sometimes form a quite prominent fringe around the stele. They vary from 1 to 2 mm. in length (outside the wood) and from 4 to 8 cells in width, spreading out fan-like towards their outer margin. The cells are radially elongated and contain numerous black globules of evident secretory nature. The tissue lying between the rays is seldom well preserved. Whatever sieve tubes that might have once existed are consistently represented by disorganized cellular fragments. The general aspect as seen in transverse section is rather similar to the expanded "phloem rays" of *M. endocentrica,* the rays in both species being characterized by their dark brown color and black secretory cells, as well as in their greater width as compared to their structure in the xylem.

As mentioned previously, numerous adventitious roots run through the cortex. They vary from tetrarch ones, which apparently originate in and run through the primary part of the stele for some distance before emerging, to triarch and pentarch ones, which seem to arise in the "periderm" adjoining the stele and follow a vertical course through the cortex for long distances before emerging. Some of these cortical roots attain considerable size (up to 2 × 2.5 cm.) and are sometimes difficult to distinguish from small steles (text-fig. 3). They are often beautifully preserved and show an aerenchymatous cortex, a feature strongly suggestive of a moist or aquatic habitat (fig. 25).

It may be pointed out here that Worsdell (1906) has found that the Cycadaceae show a similar variability in root anatomy with pentarch or tetrarch roots normally borne adventitiously near the base of the plant and the diarch and triarch roots produced towards the apex.

In Steidtmann's (1937) preliminary report he stated that M. *Noei* apparently had three large steles with at least two "star rings." Later, in his more intensive and complete treatment of the species (1944), he indicated that the structures which he had initially reported as "star rings" proved on closer observation to be "large concentric strands of the ever-present periderm." Now, our present specimen seems to show that Steidtmann's first view was the correct one and that the periderm or "cambial" rings possibly do represent developing "star rings."

De Fraine (1914) points out that the "star ring" of *M. centrofilis* differed from the star rings of the Permian stems in that it was basically protostelic while the latter, as implied by the constant reference to a "partialmark," were largely parenchymatous. This distinction is shown in pl. 10, where not only the difference between the M. *centrofilis* type of "star ring" and that of M. *stellata* is evident but also the considerable similarity between the latter and an M. *Noei* "cambial ring." Accordingly, the use of the term "star ring" for the fourth small stele in M. *centrofilis* was probably ill-advised, as it obviously had little in common with the majority of the structures so named in the Permian species but merely constituted a small independent stele. On the other hand, the evidence seems clear that in M. *Noei* we have, for the first time in a Carboniferous stem, the appearance of structures equivalent to the Permian "star rings." The fact that it was not until after a careful examination of his specimen that Steidtmann decided the structures were too similar to the profuse erratic periderm growths to be called "star rings" suggests that the "sternringen" of the poorly preserved, silicified stems of "des Rotliegenden von Chemnitz-Hilbersdorf" may also have been "periderm growths." Certainly the observable detail of the Weber & Sterzel specimens was hardly comparable to that to be found in good coal-ball material.

Steidtmann (1944) discussed the advisability of using the term "periderm" for these prolific growths, and came to the conclusion that it was valid since it did not necessarily imply suberization. However, in our specimen it can be seen that the tissue (at least that which forms many of the rings) originates in the primary part of the stele, and, instead of being an invasion from the cortex, itself produces outgrowths which occasionally penetrate the secondary wood and extrude into and through the cortex. Figure 24 shows a ring from the primary area of stele *a* (text-fig. 3) in which a certain amount of differentiation into secondary xylem has taken place, indicating that the tissue was more of a true cambial nature than periderm. That these "cambial rings," like some of the roots, originated within the stele is clearly shown by their continuous vertical course throughout the stele both above and below the occasional cortical invasions.

There is also the new evidence which has come to light in *M. Thompsonii* that the "star rings" may, in part, be derived from a *congestion* of leaf traces. Figure 59 shows a diagram of a portion of *M. Thompsonii* which has just given off a petiole. The hypodermal fiber strands are lacking on the one side and the cortical area containing the outgoing traces is considerably diminished. Arranged in a line along the stem margin in this area are numerous thin-walled xylem "rings" with a central core and radial secondary tissues (figs. 30 and 59). Successive peels, downward through the stem, show that these "rings" result from a fusion of two or more outgoing traces. It seems that the traces, while still being prolifically formed, lacked an expanding cortical area in which to scatter out, and consequently became congested and fused with a subsequent production of secondary growth. The limitations of the *M. Thompsonii* material do not allow observation of the final disposition of these "rings," but it seems likely, with the increase in the cortical area on approaching the next node, that the "rings" or "aggregate" traces may have redivided and lost their secondary wood.

If in the early ontogeny of the Permian Medullosas there were numerous leaf traces produced towards the center of the stem, the same congestion and fusion might possibly have resulted in the medullary "star rings" of *M. Solmsii*, with the central position inhibiting subsequent redivision. We are inclined to follow Worsdell (1906) rather than De Fraine (1912) in that (as pointed out in the previous discussion) we regard the Permian Medullosas as leading to the Cycads, with *Sutcliffia* as an advanced rather than primitive member of the Medullosae. The above theory of a leaf trace origin for the "star rings" would offer further evidence for Worsdell's view that the collateral rings of the Permian Medullosas and the Cycads are "composed of the one-sided remnants of a number of steles," since only in such a polystelar structure could the leaf traces be produced towards the center.

To pursue the conception still further, De Fraine (1912) states: "There appears to be no serious objection to the view that the 'meristeles' of *Sutcliffia* are homologous with the leaf trace strands which leave the stele in *M. anglica* for both appear to be entirely used up in the formation of foliar bundles." Following the same reasoning, the marginal vascular rings in *M. Thompsonii* may also be considered as homologous to the above in that they differ only in forming in the cortex rather than at the stele margin, while the Permian "star rings" may also be homologous except that they were not used up in the formation of foliar bundles due to their internal position. Thus the extra-fascicular zones and accessory cortical and pith strands (star rings) of *Medullosa*, *Sutcliffia*, and the present-day Cycads are possibly all equivalent in that they may represent aggregations of fused leaf traces around which the secondary growth has become concentric producing rings or (where adjoining groups become contiguous) forming collateral bands.

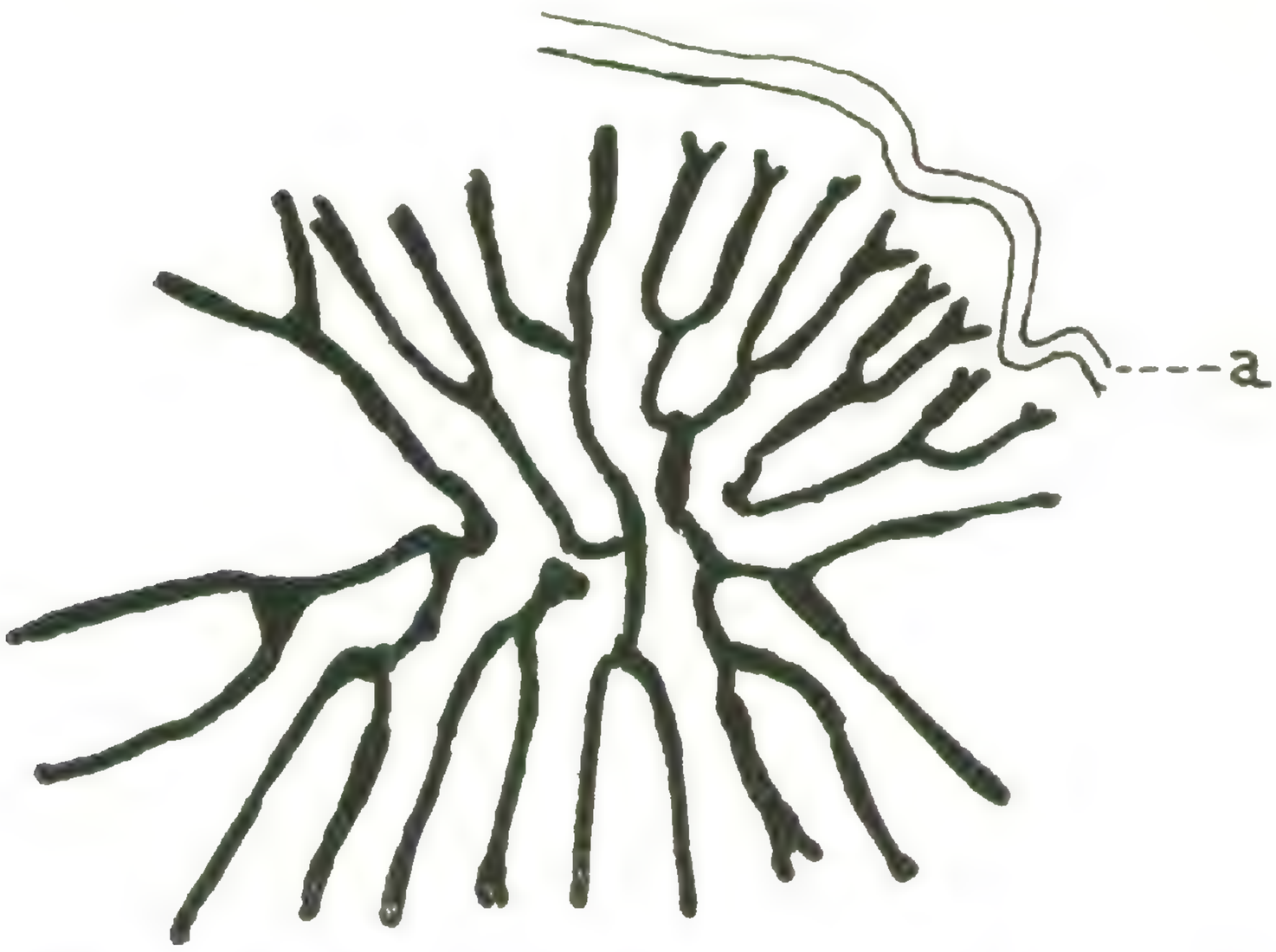
SOME MICROSPORANGIATE FRUCTIFICATIONS ASSIGNED TO THE MEDULLOSAE

The abundance and variety of *Medullosa* stem and petiole remains in the Iowa and Illinois coal balls indicate clearly that the group was a dominant and widespread feature of the Carboniferous flora. As Andrews (1948) points out: "The wide range in anatomy exhibited by the Upper Carboniferous and Permian medullosas almost certainly represents an assemblage of familial or possibly ordinal rank rather than simply a genus." Accordingly, it is not surprising to find a corresponding diversity beginning to be evidenced among the other organ genera usually associated with and regarded as belonging to the *Medullosa* stems. This is particularly true of the interesting microsporangiate fructification known as *Dolerotheca*. *Dolerotheca* is characterized by a large campanulum containing radially arranged rows of paired tubular sporangia. The evidence for its being a medullosan pollen-bearing organ is almost conclusive although it has not as yet been found attached. Dr. J. M. Schopf (1948), in addition to describing three new species from Illinois coal balls, has given a comprehensive historical, taxonomic, and phylogenetic discussion of the genus and certain allied forms. Therefore we shall limit ourselves here to describing briefly two additional new species of *Dolerotheca* from coal-ball material collected at the What Cheer Clay Products Co. coal mine, What Cheer, Iowa. This horizon is designated only as the Des Moines Series, Pennsylvanian, but as we shall point out later may be tentatively assumed to be of considerably greater age than the lowest Illinois horizon in which petrifactions of *Dolerotheca* have been found.

Dolerotheca sclerotica, sp. nov.:

The general shape is that of a broad rather shallow campanulum approximately 25 mm. in diameter and 5–7 mm. deep (fig. 45). The epidermis of the proximal sides is represented by a layer of tangentially elongated cells with conspicuous dark contents, on which are scattered a few very small capitate glandular hairs (fig. 58). Just within this layer is a definite sclerotic hypodermal zone, .4 mm. in thickness, of empty isodiametric cells, only approximately 1 out of 30 showing a black secretory plug (fig. 49). Lying immediately inside this latter zone is the parenchymatous ground tissue of the fructification which, as in the Illinois species, seems to enclose and "constitute the walls of the sporangia." It forms a network of uniform thickness, 2–3 cells, composed of thin collapsed parenchyma in which are numerous large secretory canals with their dark, opaque contents.

The double radial rows of tubular sporangia are separated by very conspicuous sclerotic bands, 4–6 cells thick, which are normally interrupted at the junction with the alternating lysigenous tubes but may occasionally form almost continuous radial septa from the center of the fructification out to the marginal ground tissue. The individual sclerotic fibers are small, 50 μ in diameter and up to 500 μ in length. The bands bifurcate from 1 to 3 times, the first time about ¼ the distance from the center, the second at about half the distance from the center,



Text-fig. 4. *Dolerotheca sclerotica:* Diagram showing pattern of bifurcations of sclerotic-fibrous framework. *a*, campanulum wall. Explanation in the text. × 4.

and the third time within 1 mm. or less of the marginal peripheral ground tissue (text-fig. 4). Additional paired rows of sporangia are intercalated at the inner bifurcations while the marginal division is generally too near the periphery to allow space for more than the insertion of a single sporangium. The lysigenous tubes are much less conspicuous than in the three Illinois species. In the latter the tubes are enclosed by walls 3–6 cells thick, having circular to oval locules, while the equivalent structures in *D. sclerotica* are represented merely by rectangular spaces between the thin (1 cell) tangential walls of adjoining sporangia (figs. 48 and 50). As in *D. formosa* Schopf, the vascular bundles of our specimen "are noteworthy for their obscurity." They consist of 3–4 small annular tracheids apparently restricted to the marginal area of the campanulum. The bundles lie in the secretory parenchymatous tissue which alternates radially with the sclerotic bands, there usually being but one bundle in each radial strand 1 mm. within the hypodermal zone.

D. sclerotica appears to have had considerably less dehiscence tissue than the Illinois species, although the distinction is possibly doubtful since our specimen was poorly preserved at the distal end. However, as shown in fig. 48, the groundwork of the fructification consists solely of the fibrous sclerenchyma bands with a parenchymatous network of secretory cells, and it is only at the extreme periphery that fragments of tissue of possible dehiscent nature are found. The sporangia average 500 × 700 μ in diameter, only the centermost being vertical. The outer sporangia originate on the ascending inner slope of the campanulum and tend to

follow the general shape, curving outward and upward (fig. 45). The spores are unusually large averaging 470 × 200 μ, in the longer dimension exceeding that of all of the Illinois species. They are marked by a monolete suture similar to that described for *D. formosa.*

The major distinctions between *D. sclerotica* and the three Illinois species—*D. villosa, D. Reedana* and *D. formosa*—are as follows:

1. Few very small capitate epidermal hairs as compared to the relatively dense pubescence of the other three species.
2. A homogeneous sclerotic hypodermal zone.
3. Lysigenous tubes which are merely gaps between thin-walled sporangia.
4. A dominating radiating framework of bifurcating fibrous sclerenchyma bands.
5. A greater amount of secretory cells in the parenchymatous ground tissue.
6. Larger prepollen or spores.

The differences may be said to be almost of generic importance and scope and lend further weight to the viewpoint voiced earlier that the Medullosae are probably a more heterogeneous group than can much longer be contained in a single genus.

Diagnosis:

A flattened campanulum up to 25 mm. in diameter. Epidermis of dark secretory cells, practically glabrous, with only a few capitate hairs. A conspicuous hypodermal zone of isodiametric sclerenchyma cells. Groundwork composed of radiating, bifurcating bands of fibrous-sclerenchyma enclosing a parenchymatous secretory tissue which composes the sporangial walls. Lysigenous tubes consisting solely of gaps between thin tangential sporangial walls.

Horizon: Des Moines Series, Pennsylvanian.

Type: Fig. 45. Slide 1628, in the paleobotanical collections of the Henry Shaw School of Botany of Washington University.

Dolerotheca Schopfii, sp. nov.:

This species, like *D. sclerotica,* is based on a single specimen also from the What Cheer coal mine near the town of What Cheer, Iowa. The fructification had evidently been broken into fragments prior to fossilization since, although cellular preservation is excellent, only an estimated one fourth or less of the campanulum was present in the coal ball. However, from the individual sporangia (up to .6 × 1.3 mm. in diameter and their incomplete length of 15 mm.) it is possible to assume that the complete structure was comparable in size to *D. formosa* and possibly more tubular due to its apparent greater depth (figs. 51 and 53). Thus, it is considerably larger than *D. sclerotica.* Unlike the latter species also, its proximal surface is covered with an extremely dense pubescence of glandular hairs up to 5–6 cells in length. The cells are flattened, 3–4 times as broad as long, the terminal cell being slightly tapered. All the cells contain black opaque secretory masses

(fig. 57). In the solid density of the hairs *D. Schopfii* is comparable to *D. villosa* but the gross appearance is closer to *D. formosa.*

Immediately within the hirsute epidermis is a broad (up to 1.5 mm. thick) hypodermal zone of large secretory canals (200 μ in diameter) scattered profusely throughout a homogeneous matrix of small fibrous sclerenchyma cells which average 50 μ in diameter to 500 μ in length. This zone is identical to and continuous with the ground tissue making up the tangential and central radial walls of the paired sporangia (figs. 46 and 47). The radiating framework of fibrous, sclerotic bands is not quite as prominent as in *D. sclerotica* but is still much more extensive than in any of Schopf's Illinois species. As in *D. sclerotica,* the radial bands are occasionally continuous for a space of 2–3 sporangia, although the more usual condition seems for the bands to have been interrupted at the point where they join the sporangial tangential walls (fig. 51). The individual fibers are approximately equal in size to those of *D. sclerotica.*

Probably the most distinctive character of the species is the apparent lack of lysigenous tubes which in the other species alternate radially with the tubular sporangia. While the fragmentary condition of the type specimen shows only a marginal portion of the original campanulum to a depth of about 6 sporangia, it can be clearly seen that the radially adjoining sporangia are separated only by a common wall of the secretory and sclerotic ground tissue (figs. 46 and 51). It is, of course, possible that this could represent an immature stage in which the cellular disintegration forming the lysigenous tubes had not yet taken place. However, the size of the fructification, which must represent considerable maturity, along with the apparent complete dehiscence of the spores, makes it seem much more likely that the lysigenous tubes were simply not developed in this species.

The vascular bundles are even more obscure than in *D. sclerotica.* They consist of only 1–2 annular tracheids and occupy a similar marginal position in the radial ground tissue just within the broad hypodermal zone.

As in *D. sclerotica,* there is no observable dehiscence tissue, which again may possibly be due to lack of sections through the distal end. Dehiscence had evidently been complete, and no spores were found in any of the sporangia.

In comparison with *D. sclerotica* and the three Illinois species the following characters of *D. Schopfii* are held to be of specific importance.

1. Absence of lysigenous tubes.

2. The broad secretory and sclerotic hypodermal zone continuous with and identical to the groundwork making up the sporangial walls.

3. The more tubular shape of the campanulum.

While the nearly glabrous stony outer tissues of *D. sclerotica* contrast strongly with the dense glandular hairs and thick secretory zone of *D. Schopfii,* the thick radial sclerotic framework in both, along with inconspicuous lysigenous tubes in *D. sclerotica* and complete lack of them in *D. Schopfii,* seems to show that the two species are much more closely related to each other than to the Illinois species.

The species is named in honor of Dr. James M. Schopf in recognition of his noteworthy work on the genus.

Diagnosis:

Campanulum an estimated 35 mm. in diameter and 15 mm. or more in depth. Proximal epidermis with a dense pubescence of broad glandular hairs; a broad hypodermal zone of large secretory canals in a homogeneous matrix of small fibrous sclerenchyma which is continuous with and identical to the groundwork forming the sporangial walls. Lysigenous tubes lacking, adjoining sporangia having a common tangential wall.

Horizon: Des Moines Series, Pennsylvanian.

Type: Fig. 51. Slide 1629 in the paleobotanical collections of the Henry Shaw School of Botany of Washington University.

Discussion:—

While accurate geological correlation of the horizon of the Des Moines Series producing these and other petrifactions described in this paper is still needed, the evidence of the fossils themselves would tend to indicate a position in the lower part of the series and possibly considerably older than the Carbondale of Illinois. This viewpoint is based on the following facts: Over a period of three years of investigating hundreds of coal balls from Illinois and Iowa (i.e., the Des Moines Series) what appear to be the more primitive plants are all from the latter horizon. *Microspermopteris aphyllum* (described earlier in this paper), with its very primitive habit and psilophytalian characters, is from the Des Moines Series; also *Medullosa primaeva* and M. *Thompsonii,* both of which have been tentatively placed at the bottom of the phylogenetic chart (text-fig. 2) as representing the most primitive stages of the known species. *Dolerotheca sclerotica* and *D. Schopfii,* with their large amount of sclerotic tissue, seem closest to *D. Reedana* which, in being from the Carbondale of Illinois, is the oldest of Schopf's three species. In addition, *D. sclerotica* and *D. Schopfii,* with their much more extreme sclerotic condition, apparent lack of dehiscence tissue, simple lysigenous tubes or complete absence of them, and larger prepollen size (in *D. sclerotica*), seem to indicate an evolutionary stage considerably below that of *D. Reedana.*

Since the much younger *Dolerotheca formosa* shows only isolated groups of sclerenchyma and *D. villosa* appears to lack them completely, the primitive state would seem to have been the almost complete radial septation (of a single telome?) by bands of fibrous sclerenchyma between which were borne the essentially independent radial rows of paired sporangia. If any other proof were necessary to show the radial rather than cyclic arrangement of the sporangia in *Dolerotheca* (Schopf, 1948) it is amply supplied in *D. sclerotica* with its almost continuous radiating network of fibrous-sclerotic bands. In addition, the more numerous and regular bifurcations of the radial framework and the nearly symmetrical intercalation of additional paired rows of sporangia seem indicative of a centrifugal direction of development.

Found in close association with *D. Schopfii* was the *Myleoxylon* fragment shown in fig. 54. A longitudinal section through its outer margin, in fact, shows the base of the fructification with its tissues apparently continuous with those of the petiole (fig. 52). While the continuity of tissues is not so complete as to allow a definite statement as to their connection, the association is extremely close and felt to be worth illustration and mention. If this condition does represent a true attachment it would seem to show that, unlike *D. Reedana, D. Schopfii* was sessile and attached directly to fairly large divisions of the rachis.

SUMMARY

1. The known Carboniferous flora is outlined and it is suggested that it falls into large tree-like, microphyllous groups and small shrubby or climbing megaphyllous groups with the pteridosperms being in the latter category. The characters of the pteridosperm stem genera are given, and it is emphasized that they constitute a clearly defined group irrespective of the lack of knowledge as to whether they bore seeds or sporangia.

2. A new unique plant based on a stem with pteridosperm characters is described and discussed. Named *Microspermopteris aphyllum* because of its very small size and leafless condition it offers evidence for the origin of the seed-ferns from the Psilophytales, as well as for megaphyllous leaf development. It combines characters of both *Lyginopteris* and *Heterangium* and appears to have possibly been ancestral to both.

3. Three new species of *Medullosa* are described, and a new phylogenetic viewpoint presented. The evidence for a climbing or creeping habit for the group is given, new evidence being offered for a bilateral, dorsi-ventral habit.

4. Some excellent new material of *Medullosa Noei* is described with particular reference to new data on the conspicuous phloem rays, adventitious aerenchymatous roots, and periderm or "cambial" rings which appear similar to the star rings of the Permian species. "Star rings" are discussed in general, and it is shown that the fourth small stele of *Medullosa centrofilis* had nothing in common with the "star rings" of the Permian plants. "Aggregate leaf traces" in *Medullosa Thompsonii* are described and compared to Permian "star rings."

5. The microsporangiate fructifications of *Medullosa* are discussed and two new species of *Dolerotheca* are described. Evidence is offered that they constitute the most primitive of the known species and show additional proof of a radial rather than cyclic arrangement of the tubular sporangia. A very close association with possible attachment is illustrated for a *Dolerotheca* and *Myleoxylon*. It is also suggested that the plant remains from the Iowa coal balls may be of some aid in a more accurate determination of the horizon of the Des Moines Series.

ACKNOWLEDGMENT

The author wishes to recognize the constructive guidance of Dr. Henry N. Andrews under whose direction the present work was conceived and carried out.

Thanks are also due Mr. Frederick O. Thompson of Des Moines, Iowa, for his extensive coal-ball collections which provided much of the investigated material, as well as to Dr. J. M. Schopf and R. M. Kosanke, for their cooperation on the *Dolerotheca* section.

BIBLIOGRAPHY

Andrews, Henry N. (1940). On the stelar anatomy of the pteridosperms, with particular reference to the secondary wood. Ann. Mo. Bot. Gard. **27**:51–118.

————, (1945). Contributions to our knowledge of American Carboniferous floras. VII. Some pteridosperm stems from Iowa. *Ibid.* **32**:323–360.

————, (1948). Some evolutionary trends in the pteridosperms. Bot. Gaz. **110**:13–31.

————, and Kernen, J. A. (1946). Contributions to our knowledge of American Carboniferous floras. VIII. Another *Medullosa* from Iowa. Ann. Mo. Bot. Gard. **33**:141–146.

Arnold, C. A. (1940). Structure and relationship of some Middle Devonian plants from western New York. Am. Jour. Bot. **27**:57–63.

————, (1947). An Introduction to Paleobotany. New York.

————, (1948). Classification of gymnosperms from the viewpoint of paleobotany. Bot. Gaz. **110**:1–12.

Benson, M. (1933). On the roots and habit of *Heterangium Grieii*. Ann. Bot. **47**:313–315.

Bower, F. O. (1930). Size and Form in Plants. London.

De Fraine, E. (1912). On the structure and affinities of *Sutcliffia*, in the light of a newly discovered specimen. Ann. Bot. **26**:1031–1066.

————, (1914). On *Medullosa centrofilis*, a species of *Medullosa* from the Lower Coal Measures. *Ibid.* **28**:251–264.

Halle, T. G. (1916). Lower Devonian plants from Röragen in Norway. Kgl. Svenska Vetenskapsakad. Handl. **57**:1–43, *pl. 1–4*.

Hirmer, Max (1933). Zur Kenntnis der Structurbietenden Pflanzenreste des jungeren Palaeozoikums. Palaeontographica *77*, Abt. B.

Hoeg, O. A. (1937). The Devonian floras and their bearing upon the origin of vascular plants. Bot. Rev. **3**:563–592.

Lignier, O. (1908). Essai sur l'evolution morphologique de règne végétal. Soc. Linn. Normandie, Bull. VI, **3**:35–62.

Sahni, B. (1920). On the structure and affinities of *Acmopyle Pancheri* Pilger. Roy. Soc. (London), Phil. Trans. B. **210**:253–310.

Schopf, J. M. (1939). *Medullosa distelica*, a new species of the Anglica group of *Medullosa*. Am. Jour. Bot. **26**:196–207.

————, (1948). Pteridosperm male fructifications: American species of *Dolerotheca*, with notes regarding certain allied forms. Jour. Paleont. **22**[6]:681–724, *pls. 104–115*.

Scott, D. H. (1899). On the structure and affinities of fossil plants from the Palaeozoic rocks. 3. On *Medullosa anglica*, a new representative of the Cycadofilicales. Roy. Soc. (London), Phil. Trans. B. **191**:81–126.

————, (1914). On *Medullosa pusilla*. Roy. Soc. Lond. Proc. B. **87**:221–228.

————, (1917). The Heterangiums of the British Coal Measures. Jour. Linn. Soc. (London), Bot. **44**:59–104, *pl. 1–4*.

————, (1923). Studies in Fossil Botany. London.

Seward, A. C. (1917). Fossil Plants. Vol. 3. Cambridge Univ.

Solereder, H. (1908). Systematic anatomy of the Dicotyledons. Vol. 2. Oxford.

Steidtmann, W. E. (1937). A preliminary report on the anatomy and affinities of *Medullosa Noei* sp. nov., from the Pennsylvanian of Illinois. Am. Jour. Bot. **24**:124–125.

————, (1944). The anatomy and affinities of *Medullosa Noei* Steidtmann, and associated foliage, roots, and seeds. Univ. Mich., Contrib. Mus. Paleont. **6**:131–166.

Thiessen, R. (1920a). Composition and compilation of bituminous coals. Jour. Geol. **28**:*pl. 11*, *fig. 42*.

————, (1920b). Structure in Paleozoic bituminous coals. U. S. Bur. Mines, Bull. 117:*pl. 151*, *fig. A-B*, *pl. 152*, *153*.

Weber, O., und Sterzel, J. T. (1896). Beträge zur Kenntnis der Medulloseae. Naturwiss. Ges. Chemnitz, Ber. **13**:44–143.

Westermaier, M., und Ambronn, H. (1881). Beziehungen zwischen Lebensweise und Structur der Schling- und Kletterpflanzen. Flora **64**:417–430.

Wilson, Carl L. (1942). The Telome Theory and the origin of the stamen. Am. Jour. Bot. **29**:759–764.

Worsdell, W. C. (1906). The structure and origin of the Cycadaceae. Ann. Bot. **20**:129–159.

EXPLANATION OF PLATE

PLATE 2

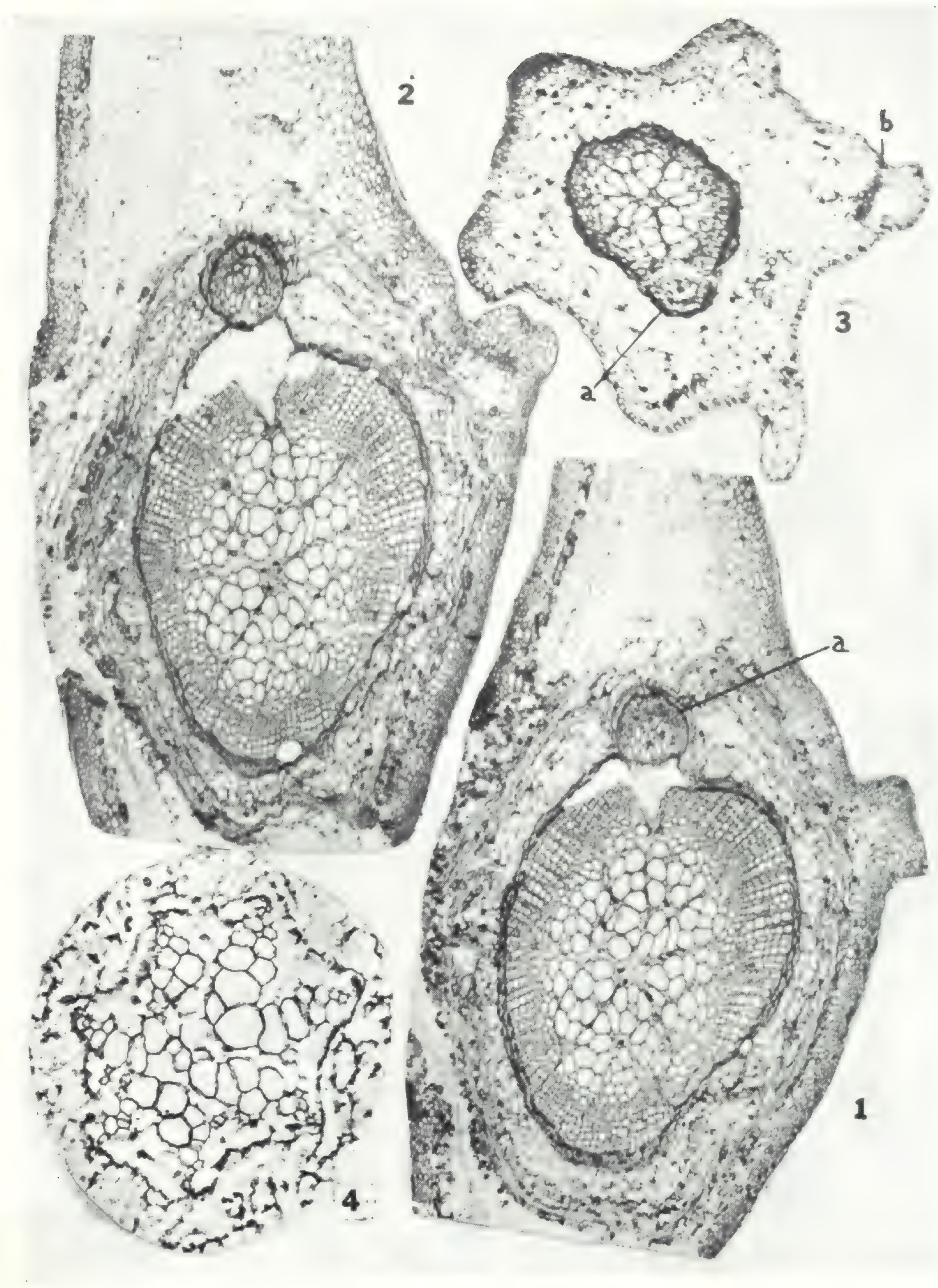
Microspermopteris aphyllum

Fig. 1. Cross-section of a mature stem showing departure of a collateral branch bundle. From slide 1602, × 20.

Fig. 2. Same specimen a few peels above the preceding figure. Branch bundle is becoming concentric. From slide 1603, × 20.

Fig. 3. Cross-section of a small stem (branch?): *a*, beginning of branch vascular bundle departure; *b*, sclerotic plate. (See fig. 55 which shows a later stage of branch bundle departure on same stem). From slide 1604, × 20.

Fig. 4. Enlargement of the stele of a heptarch adventitious root. (See fig. 56 for appearance of complete cross-section). From slide 1605, × 50.



BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

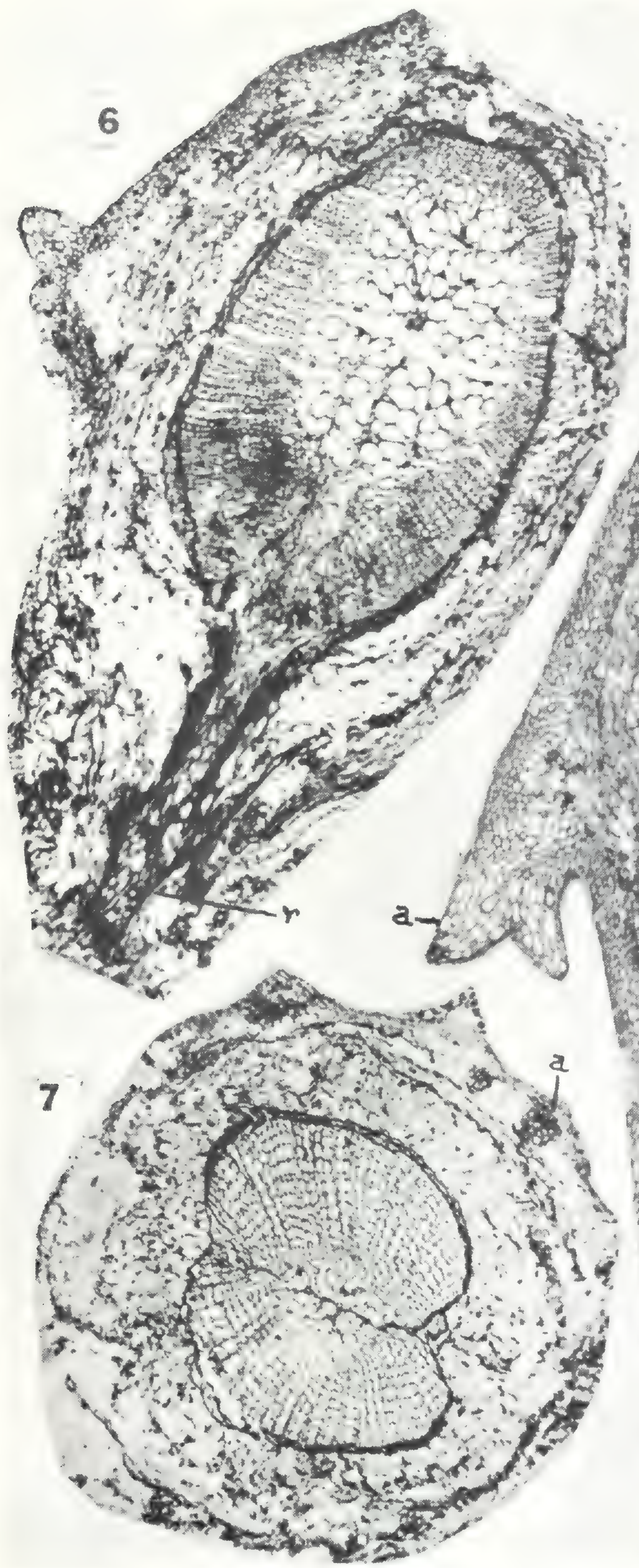
PLATE 3

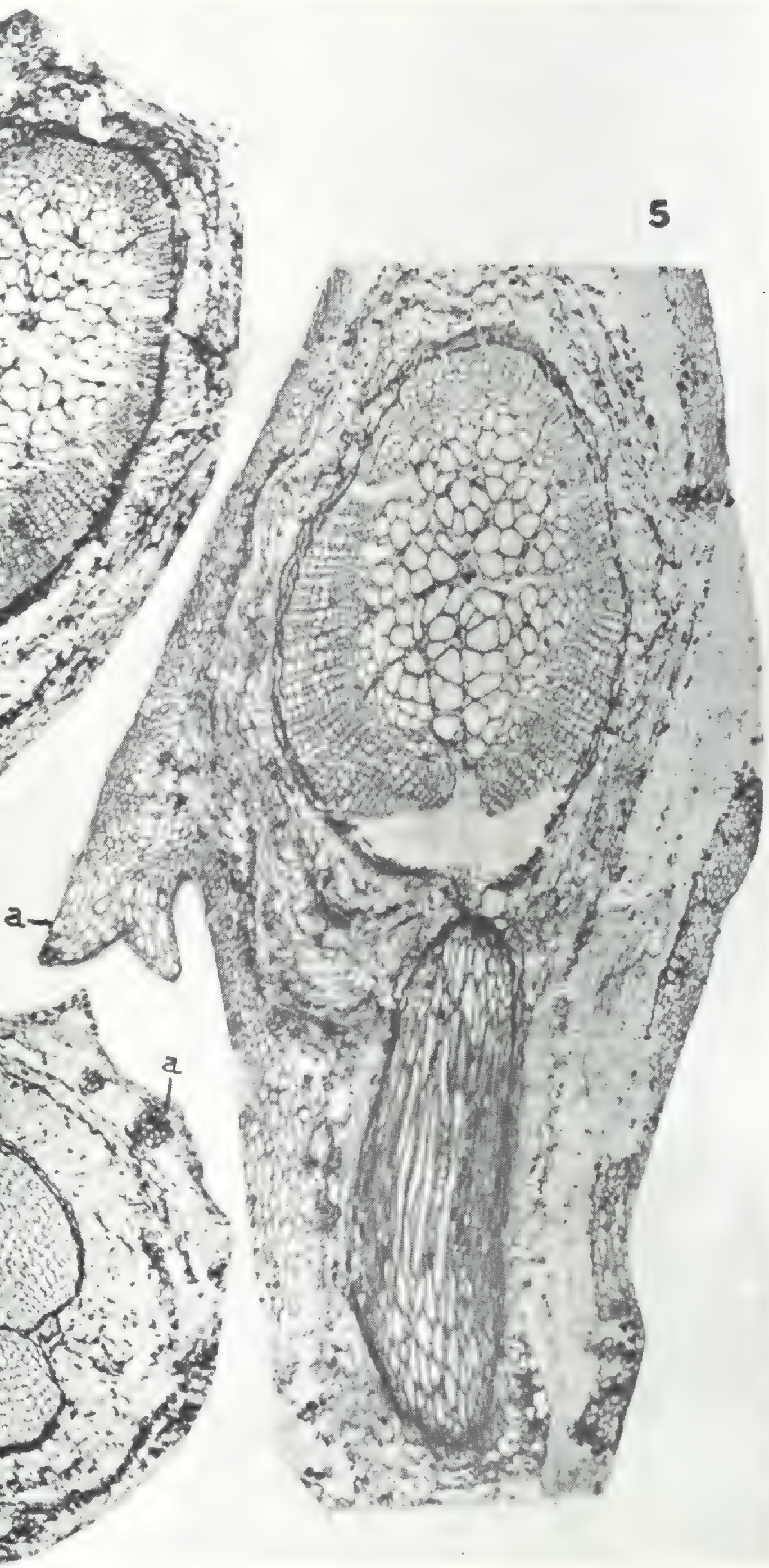
Microspermopteris aphyllum

Fig. 5. Cross-section of same stem as in figs. 1 and 2, showing the horizontal passage of the branch vascular bundle; *a*, forked emergence. From slide 1606, × 18.

Fig. 6. Cross-section taken a few peels above the preceding figure showing departure of an adventitious root; root (*r*) has curved downwards and out of the cortex. From slide 1607, × 18.

Fig. 7. Cross-section of a more mature stem showing unequal xylem development; *a*, sclerotic plate just within the epidermis. From slide 1608, × 15.





BAXTER—FOSSIL PTERIDOSPERMS

Explanation of Plate

PLATE 4

Microspermopteris aphyllum

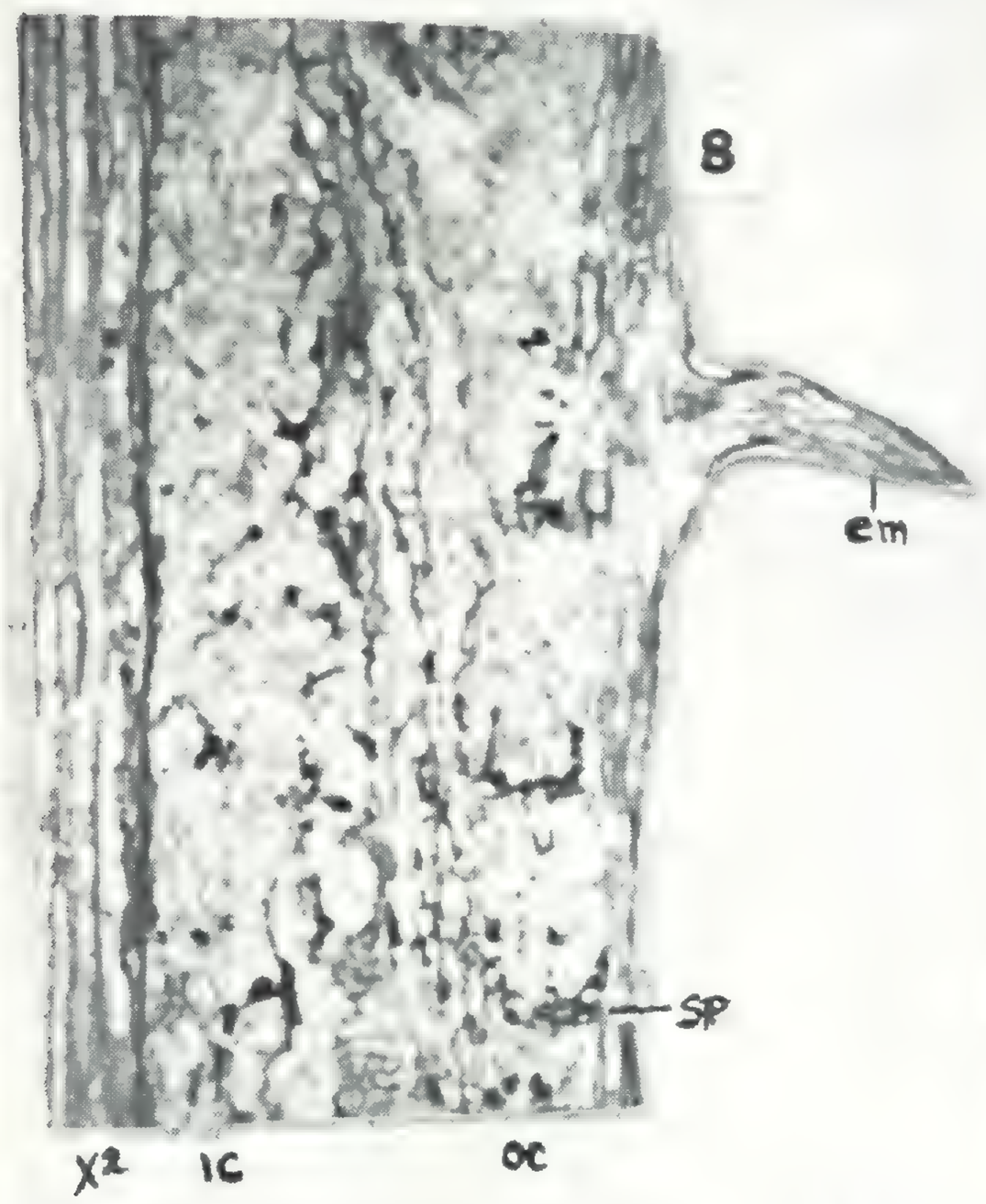
Fig. 8. Radial section of stem: x^2, secondary xylem; *IC*, inner cortex; *OC*, outer cortex; *SP*, sclerotic plate; *em*, emergence. From slide 1609, × 50.

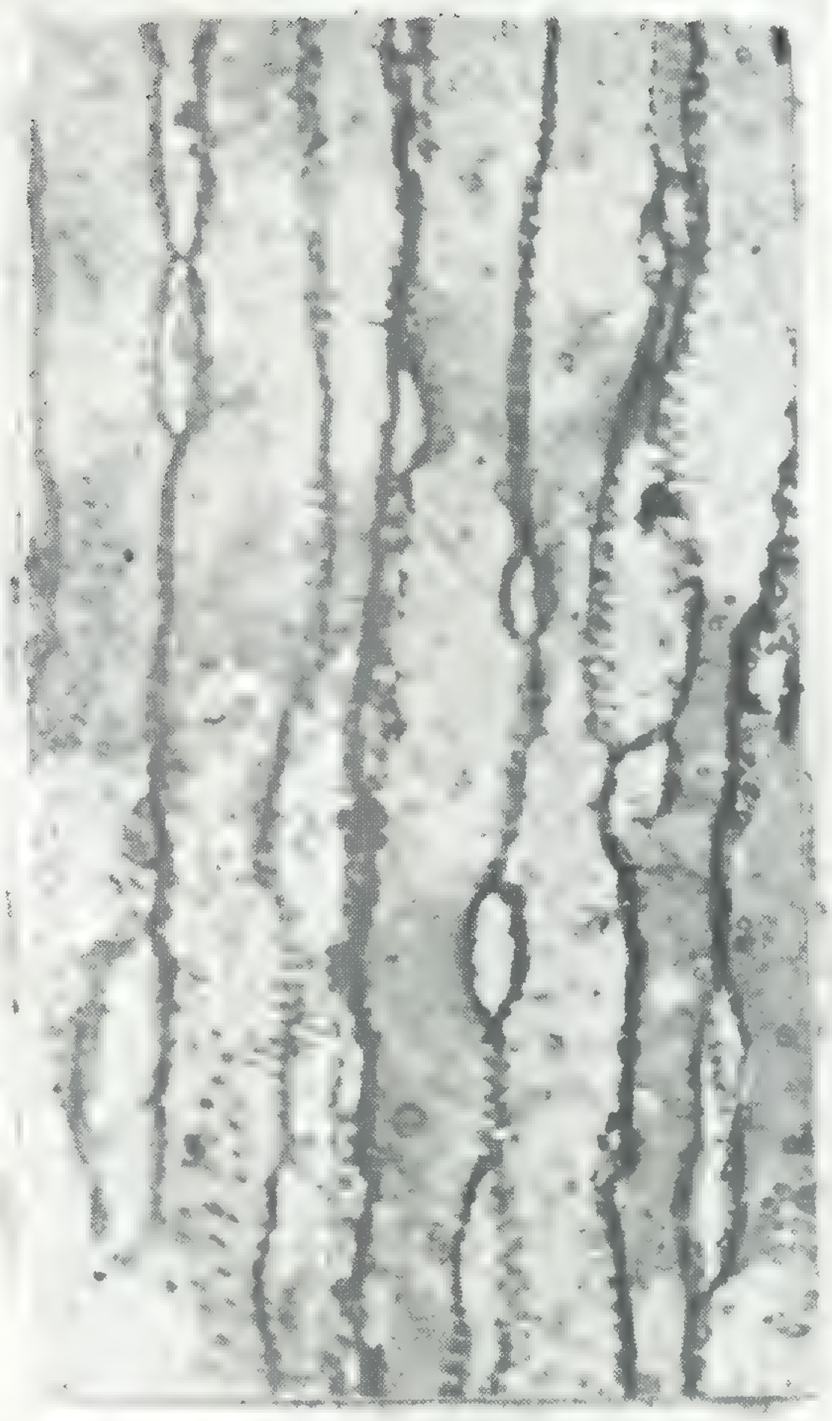
Fig. 9. Tangential view of secondary wood showing small uniseriate rays and pitting in tangential walls. From slide 1610, × 135.

Fig. 10. Radial section of stem showing sclerotic plates in outer cortex just within epidermis. From slide 1611, × 53.

Fig. 11. Tangential section through outer cortical zone showing anastamosing horizontal plates. From slide 1612, × 25.

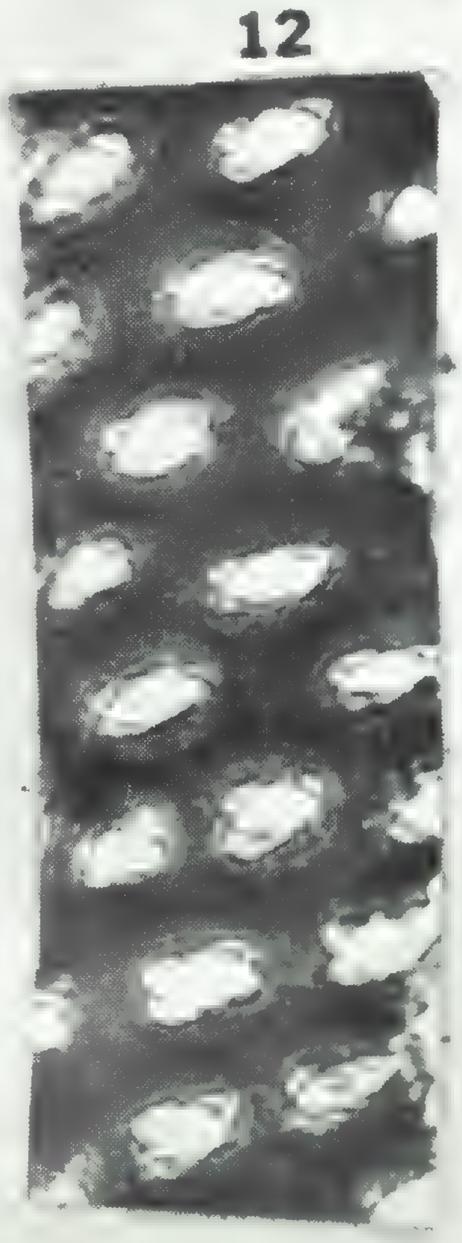
Fig. 12. Reticulate bordered pitting in wall of a metaxylem tracheid. From slide 1613, × 450.


8
em
SP
X²
IC
OC


9

10

11


12

Explanation of Plate

PLATE 5

A partial reconstruction of *Microspermopteris aphyllum*, × 4. Explanation in text.

BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

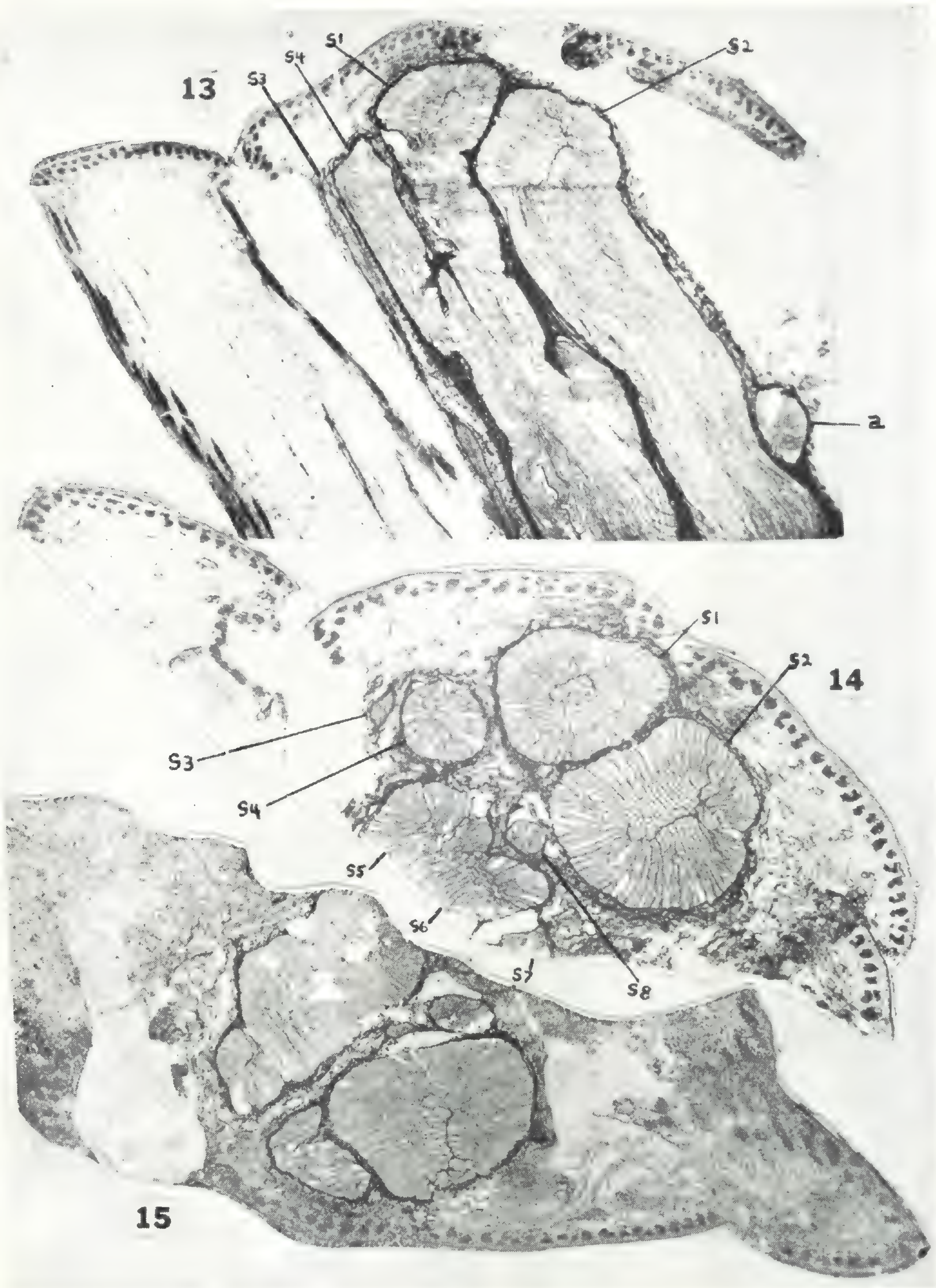
PLATE 6

Medullosa primaeva

Fig. 13. Transverse-longitudinal view of type specimen showing branching and fusing of the steles: *a*, small stele in a horizontal course through the stem; *S1*, *S2*, *S3*, and *S4* show portions of steles indicated in next figure. From slide 1614, × 4.5.

Fig. 14. Transverse section of top surface of type specimen: *S1*, *S2*, *S3*, *S4*, *S5*, *S6*, *S7*, and *S8* indicate the eight steles. From slide 1615, × 6.2.

Fig. 15. Transverse section of bottom surface of type specimen. Steles have partially fused. From slide 1616, × 6.2.


13
S1
S2
S3
S4
a
S1
S2
S3
S4
S5
S6
S7
S8
14
15

EXPLANATION OF PLATE

PLATE 7

Medullosa elongata

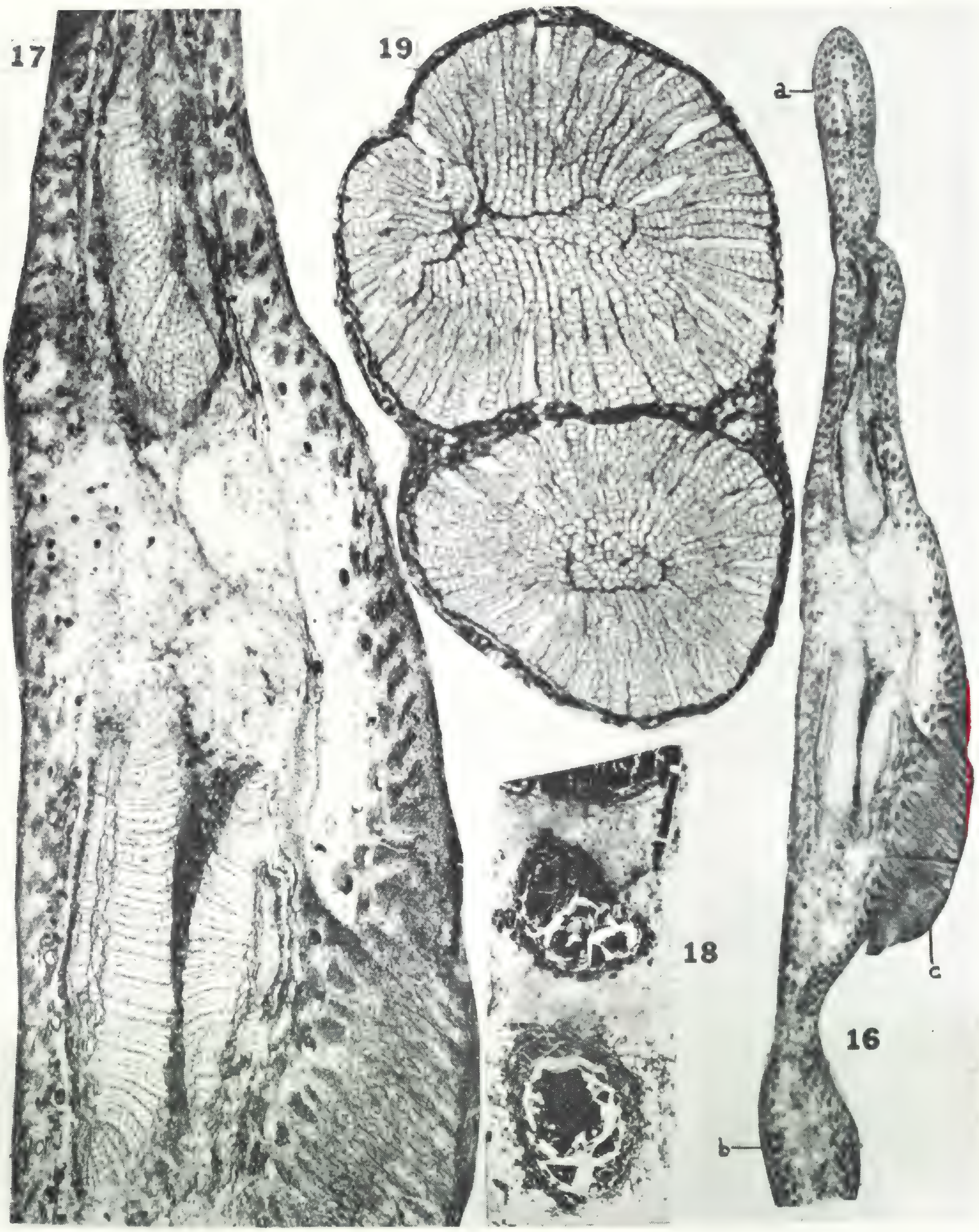
Fig. 16. Transverse view of complete type specimen: *a* and *b*, lateral leaf bases; *c*, dorsal leaf base. From slide 1617, × 2.5.

Fig. 17. Enlargement of central portion of stem shown in fig. 16 to show the details of the three steles. Note narrow line of primary wood in lower left-hand stele. From slide 1617, × 6.5.

Fig. 18. Compound resin canals which run horizontally through the stem. From slide 1618, × 6.5.

Medullosa primaeva

Fig. 19. Enlargement of steles *S1* and *S2* from fig. 14. Note almost solid protosteles. From slide 1615, × 16.



BAXTER—FOSSIL PTERIDOSPERMS

Explanation of Plate

PLATE 8

Medullosa endocentrica

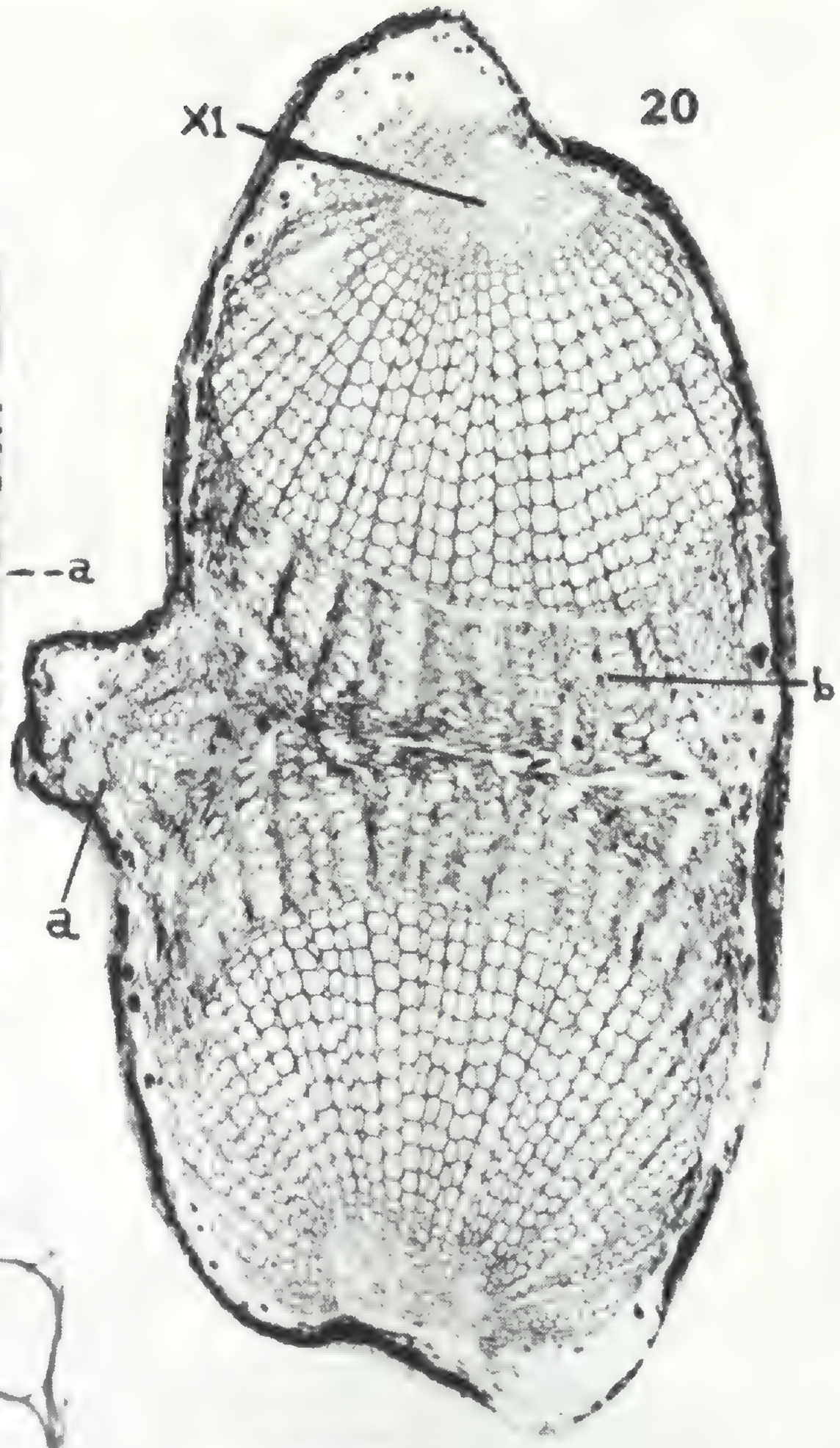
Fig. 20. Transverse section of stelar assembly of type specimen with enclosing "periderm": *a*, third small stele; *b*, phloem zone; *XI*, primary xylem. From slide 1619, × 10.

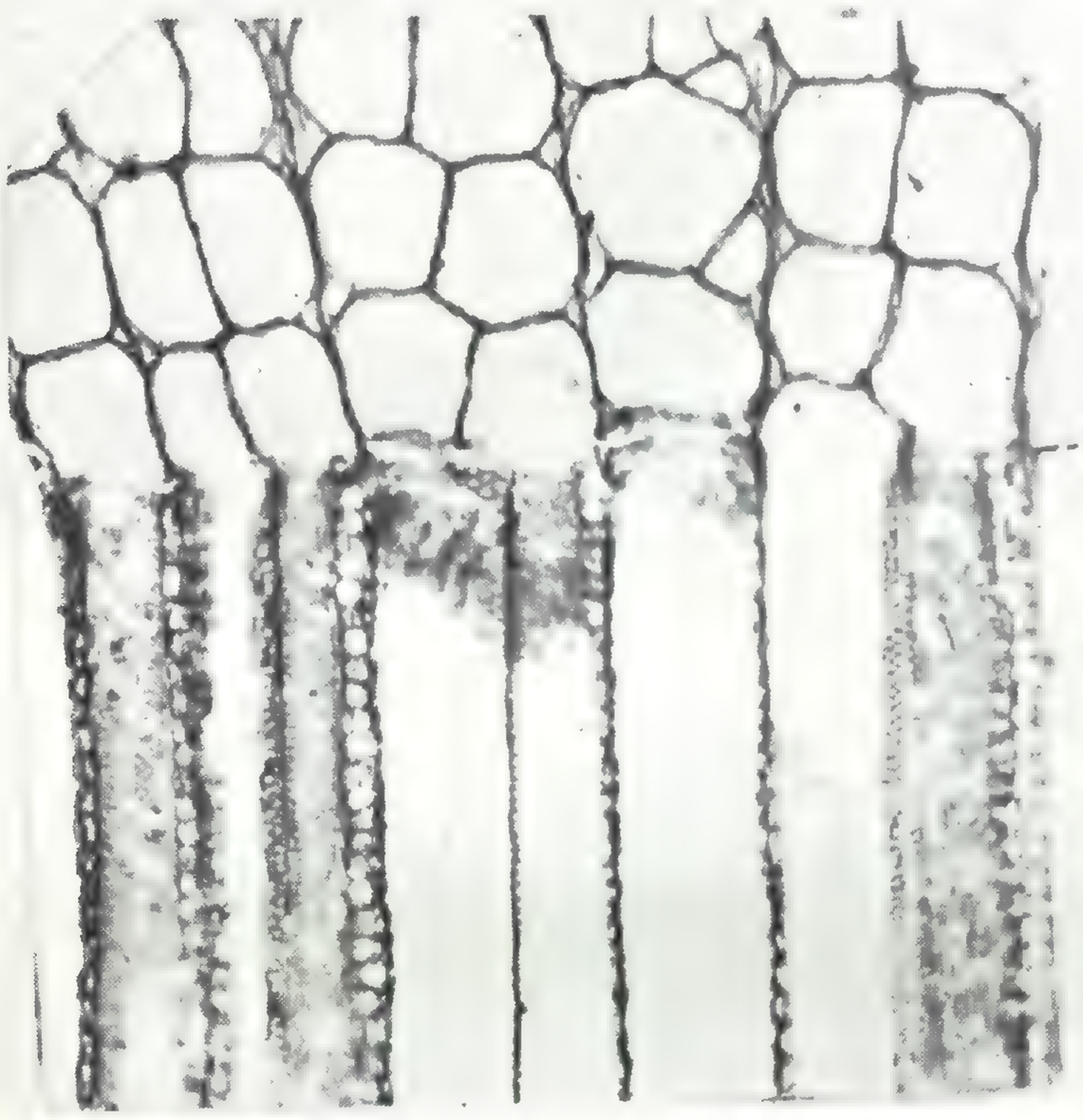
Fig. 21. Transverse-tangential section showing very broad rays in "phloem" area. Above point indicated by *(a)* is transverse, below tangential. From slide 1620, × 40.

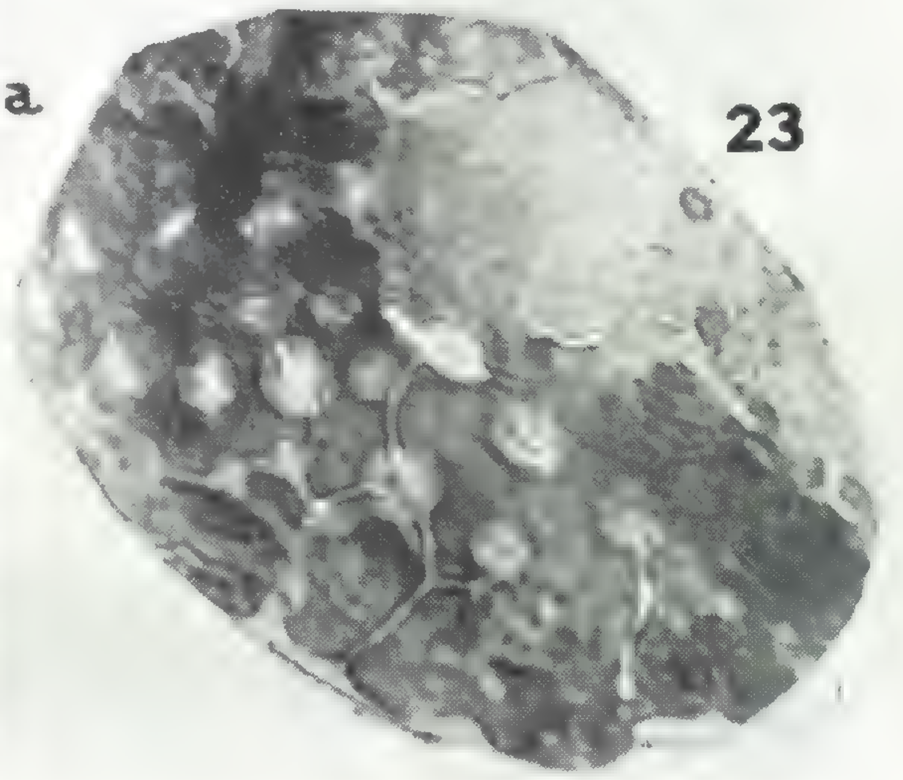
Fig. 22. Tangential-transverse section through secondary xylem showing narrow (1–2 cells wide) rays; *a* indicates line between transverse and tangential views. From slide 1621, × 40.

Fig. 23. Portion of a transverse "sieve plate" from one of the large "sieve tubes" of the phloem zone. From slide 1620, × 650.

21
a


X1
20
a
b


22
a


23

Explanation of Plate

PLATE 9

Medullosa Noei

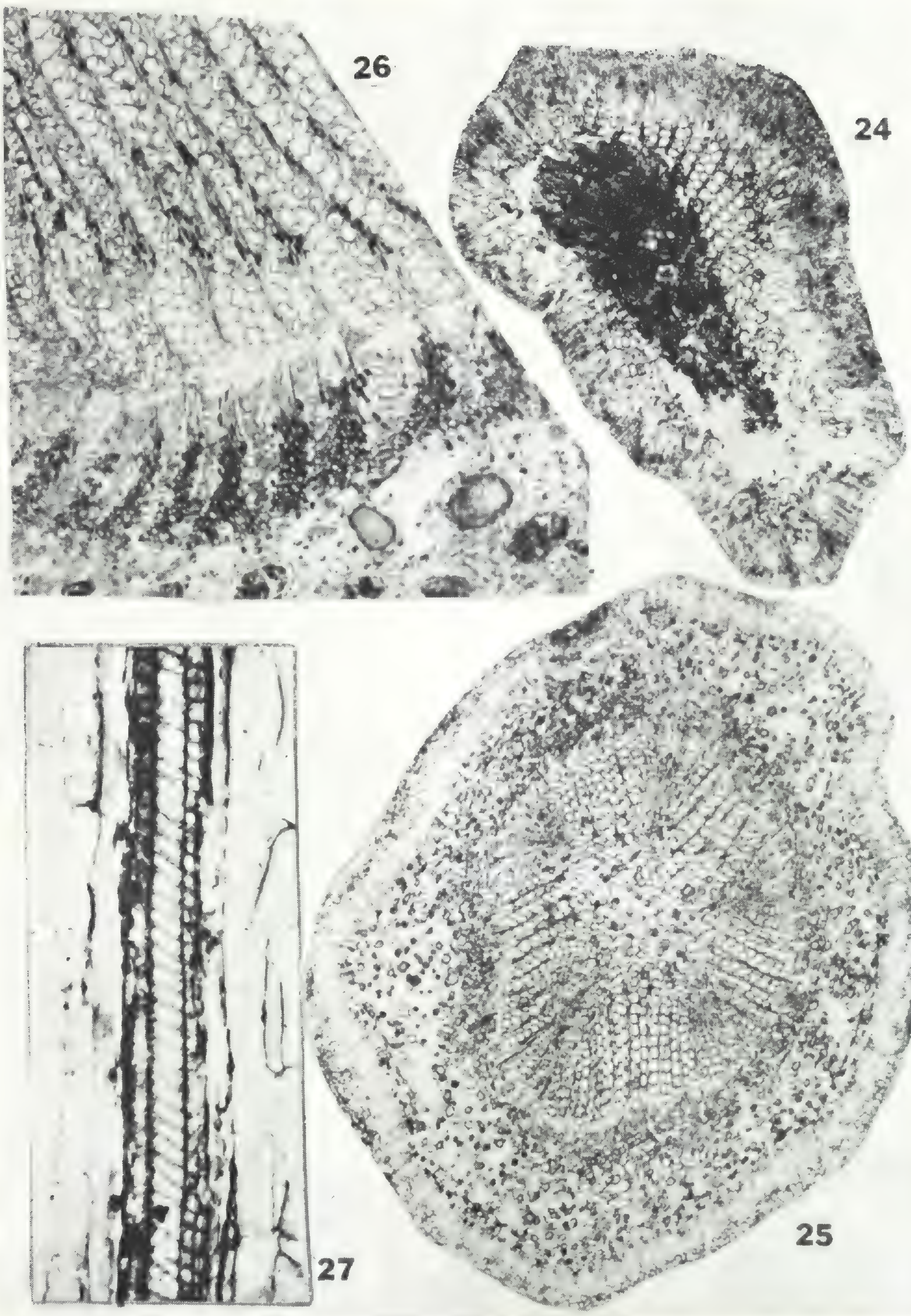
Fig. 24. A single "cambial ring" showing development of secondary wood. Dark central area is composed of primary tracheids and parenchyma. From slide 1622, × 9.

Fig. 25. A single well-preserved cortical, pentarch root. Note enclosing periderm and aerenchymatous cortex. From slide 1623, × 14.

Fig. 26. Marginal portion of a stele showing fringe of expanded phloem rays. From slide 1624, × 12.

Medullosa primaeva

Fig. 27. Longitudinal section through cortex showing spiral thickening in a leaf trace. From slide 1625, × 95.



BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

PLATE 10

"Star Rings"

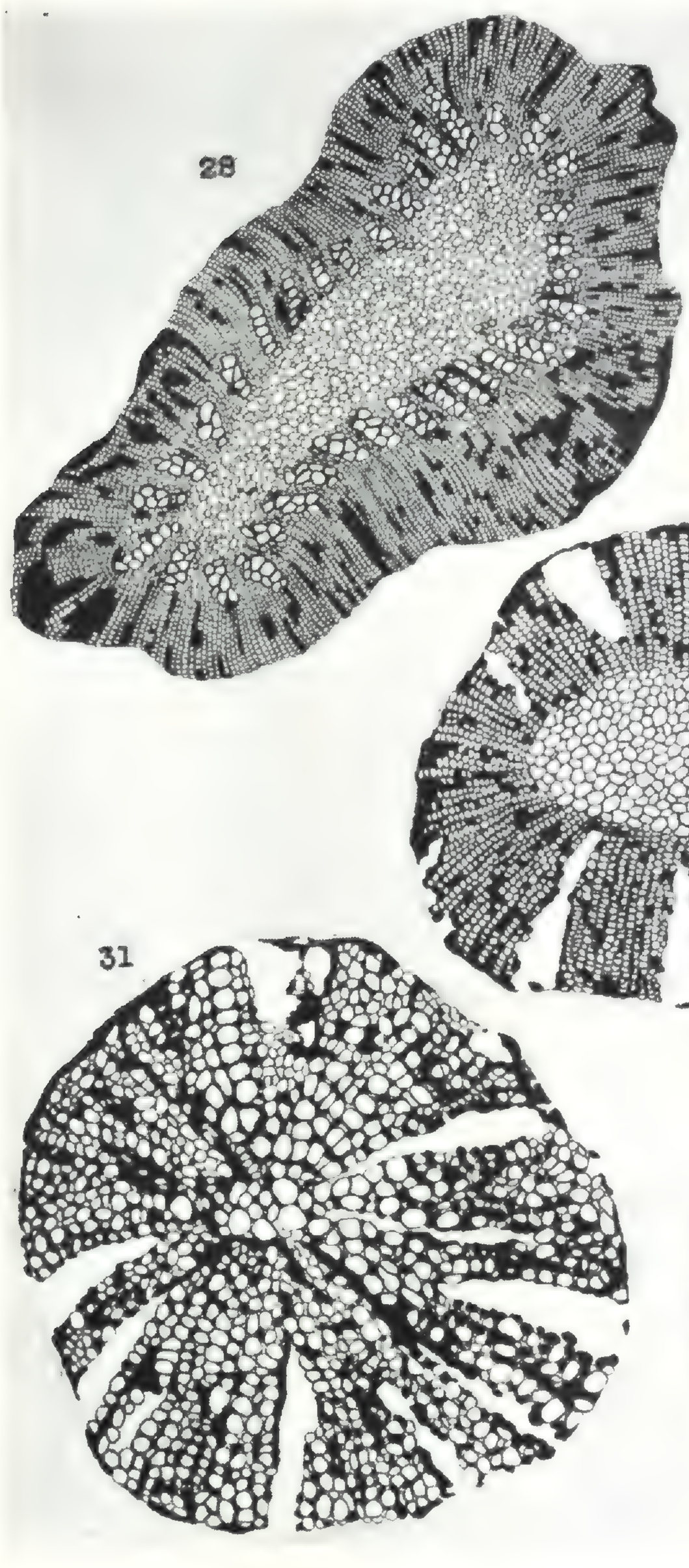
Fig. 28. A "cambial" or "periderm" ring from M. *Noei* in which radial rows of secondary xylem have formed. From slide 1622, × 5.5.

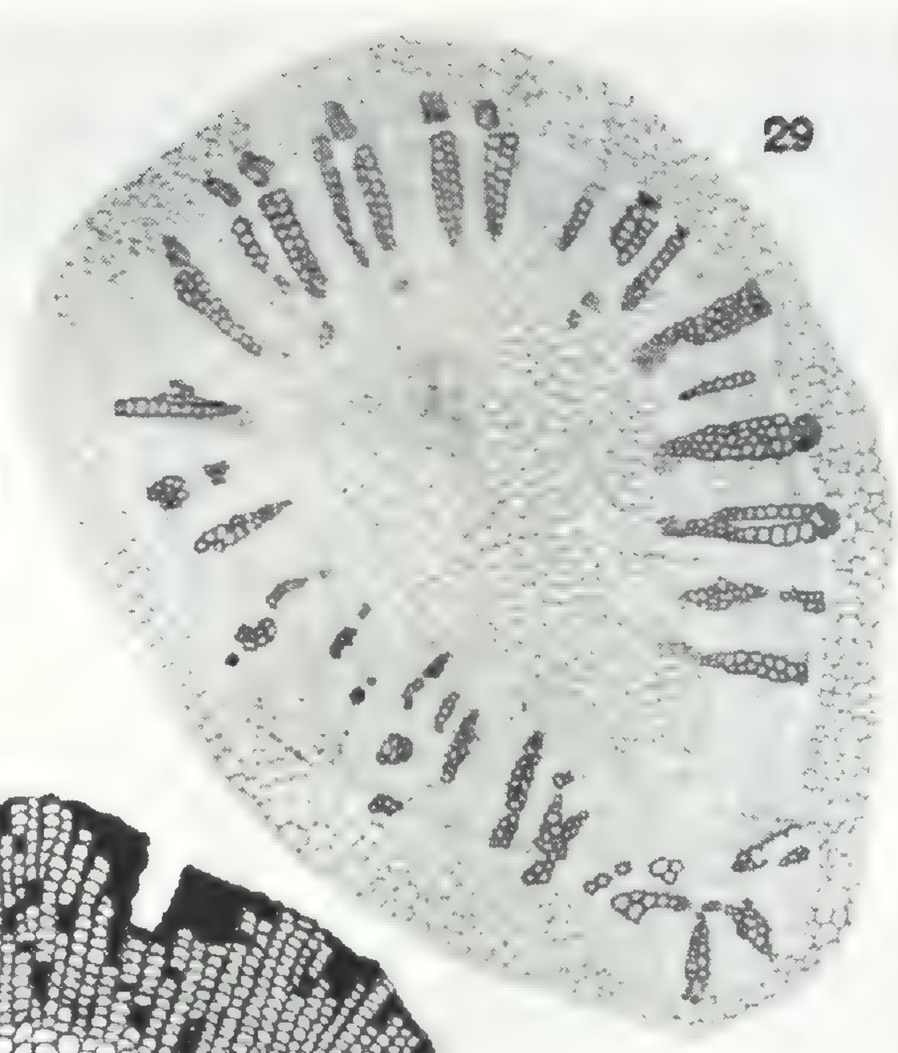
Fig. 29. A "star ring" from M. *stellata* v. Cotta a. *typica*, at the same magnification as the above (after Weber and Sterzel), × 5.5.

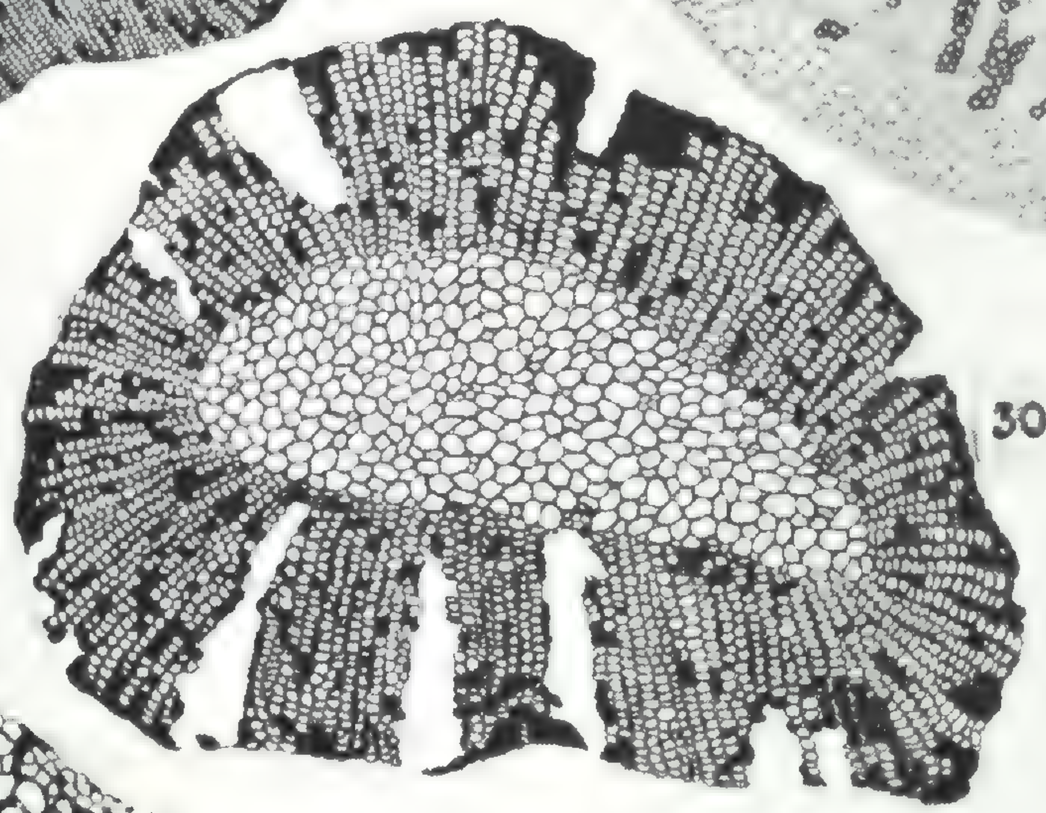
Fig. 30. An "aggregate leaf trace" from M. *Thompsonii* (see fig. 59b). From slide 1626, × 13.7.

Fig. 31. A single small stele of M. *primaeva*. From slide 1615, × 20.7.

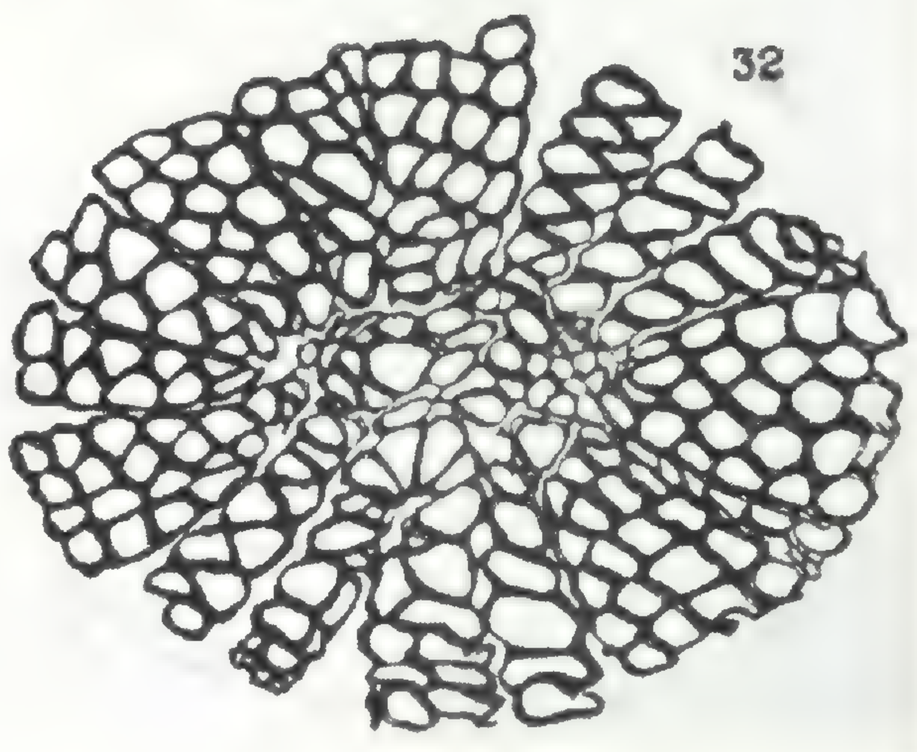
Fig. 32. "Star Ring" of M. *centrofilis* (after De Fraine), × 20.7.


28


29


30

31


32

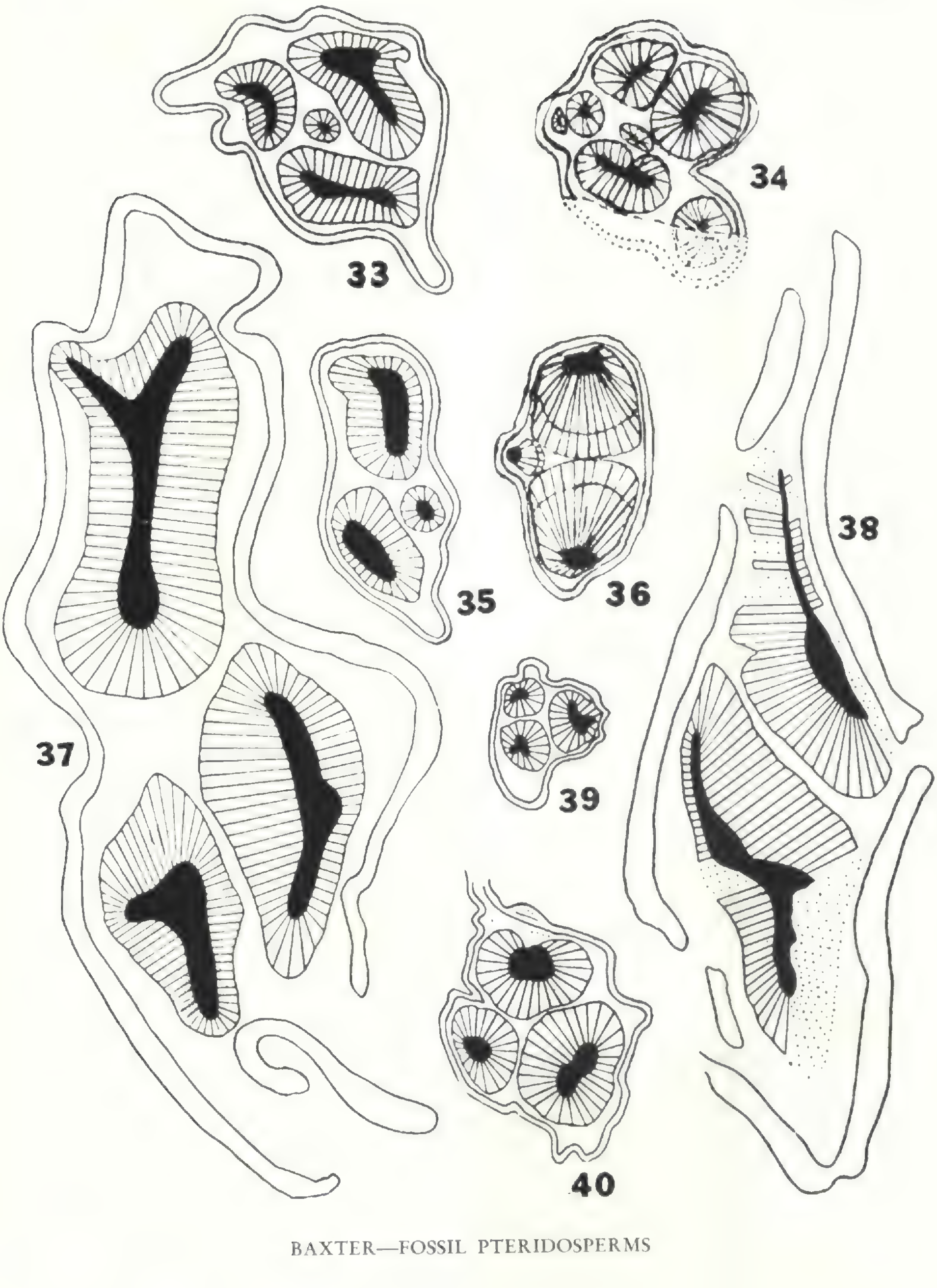
Explanation of Plate

PLATE 11

Diagrams of the stelar assemblies with enclosing periderm (where present) of all of the Carboniferous species of *Medullosa* with the exception of *M. Leuckarti.* The magnification is 2.8, and all of the diagrams other than figs. 34, 36, 42, and 43 are taken from Andrews (1945, 1946). The primary area of the stele is shown as solid black, the secondary wood as radiating lines, and the periderm as enclosing double or dotted lines depending on whether it was actually observed or was partially assumed.

Fig. 33. *M. centrofilis* De Fraine; Fig. 34. *M. primaeva* Baxter; Fig. 35. *M. Thompsonii* Andrews; Fig. 36. *M. endocentrica* Baxter; Fig. 37. *M. anglica* Scott; Fig. 38. *M. distelica* Schopf; Fig. 39. *M. pusilla* Scott; Fig. 40. *M. anglica* var. *Thiessenii* Schopf.

(Continued on pl. 12)

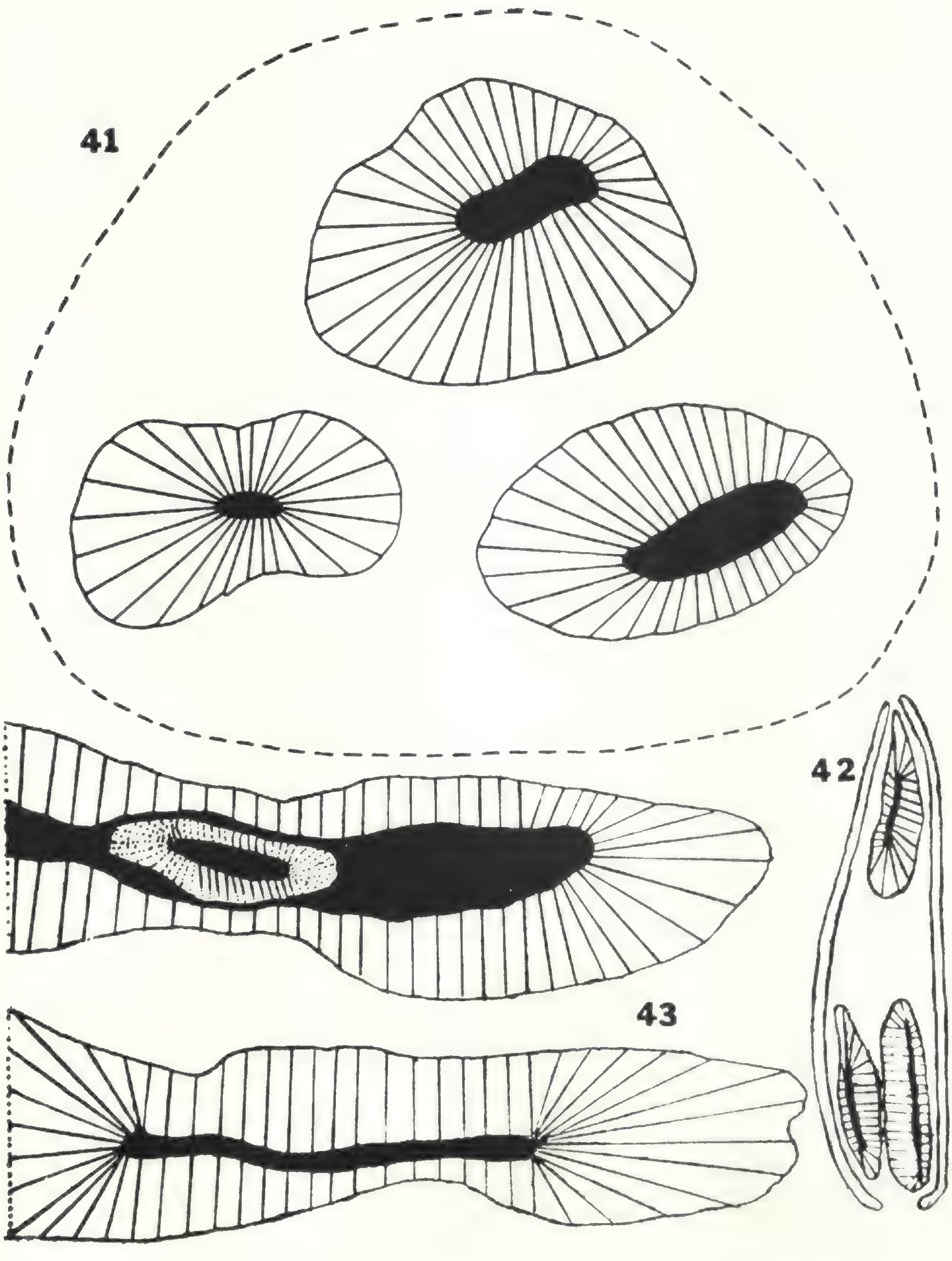


BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

PLATE 12

Fig. 41. *M. anglica* var. *ioensis* Andrews; Fig. 42. *M. elongata* Baxter; Fig. 43. *M. Noei* Steidtmann, showing only about half of two of the stem's three steles. (*M. Noei* is so much larger than any of the other species represented here that one complete stele at × 2.8 magnification would more than fill an entire plate.) The white ring within the black primary area (in the upper of the two stele halves) represents a "cambial ring" as shown in figs. 24 and 28.

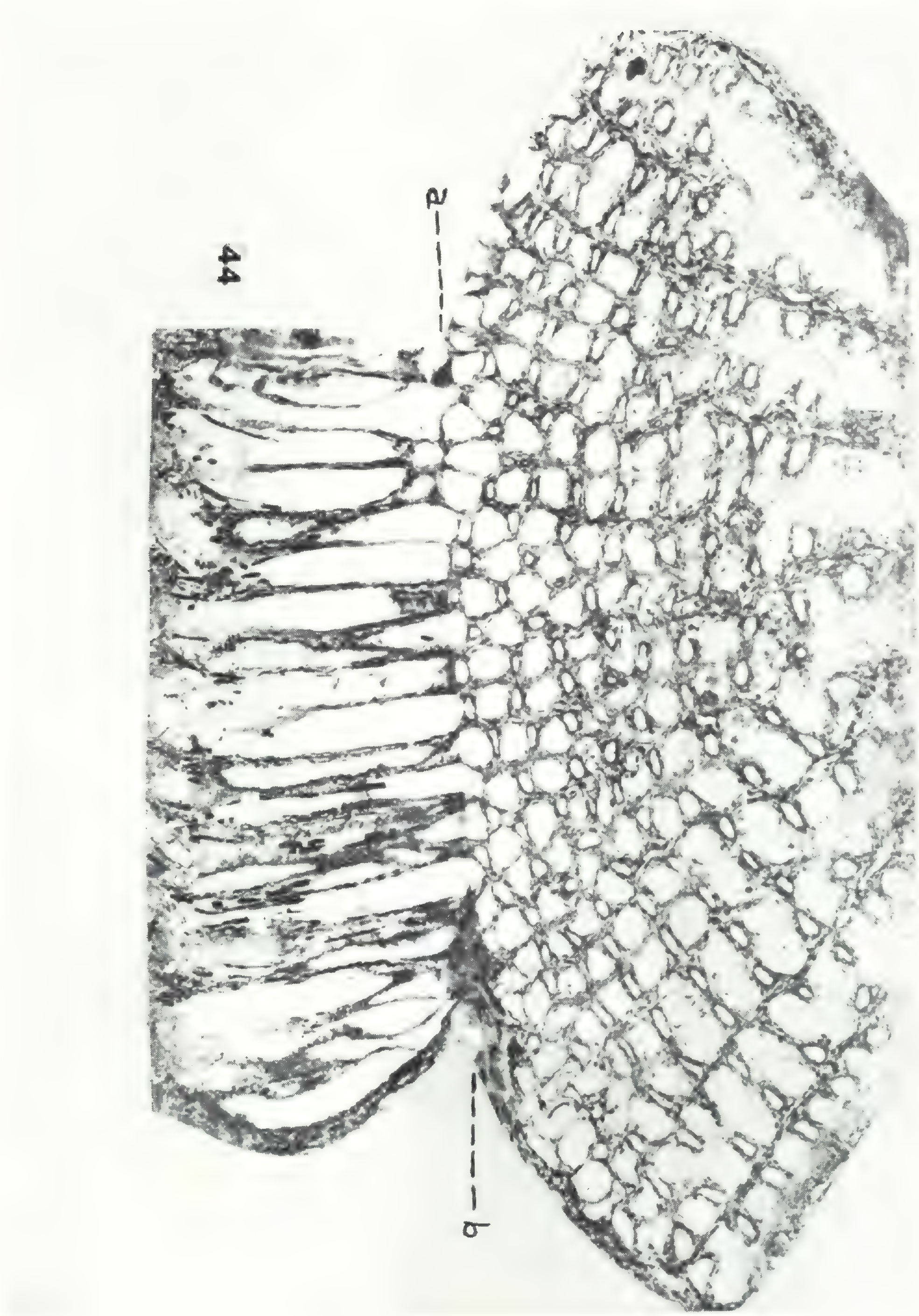

41
42
43

Explanation of Plate

PLATE 13

Dolerotheca formosa

Fig. 44. Transverse-longitudinal view of a portion of a complete campanulum. Below the line *a-b* is the longitudinal cut; above, the transverse. In comparison with the following figure note the large lysigenous tubes and absence of a strong sclerotic framework. From slide 1627, × 9.

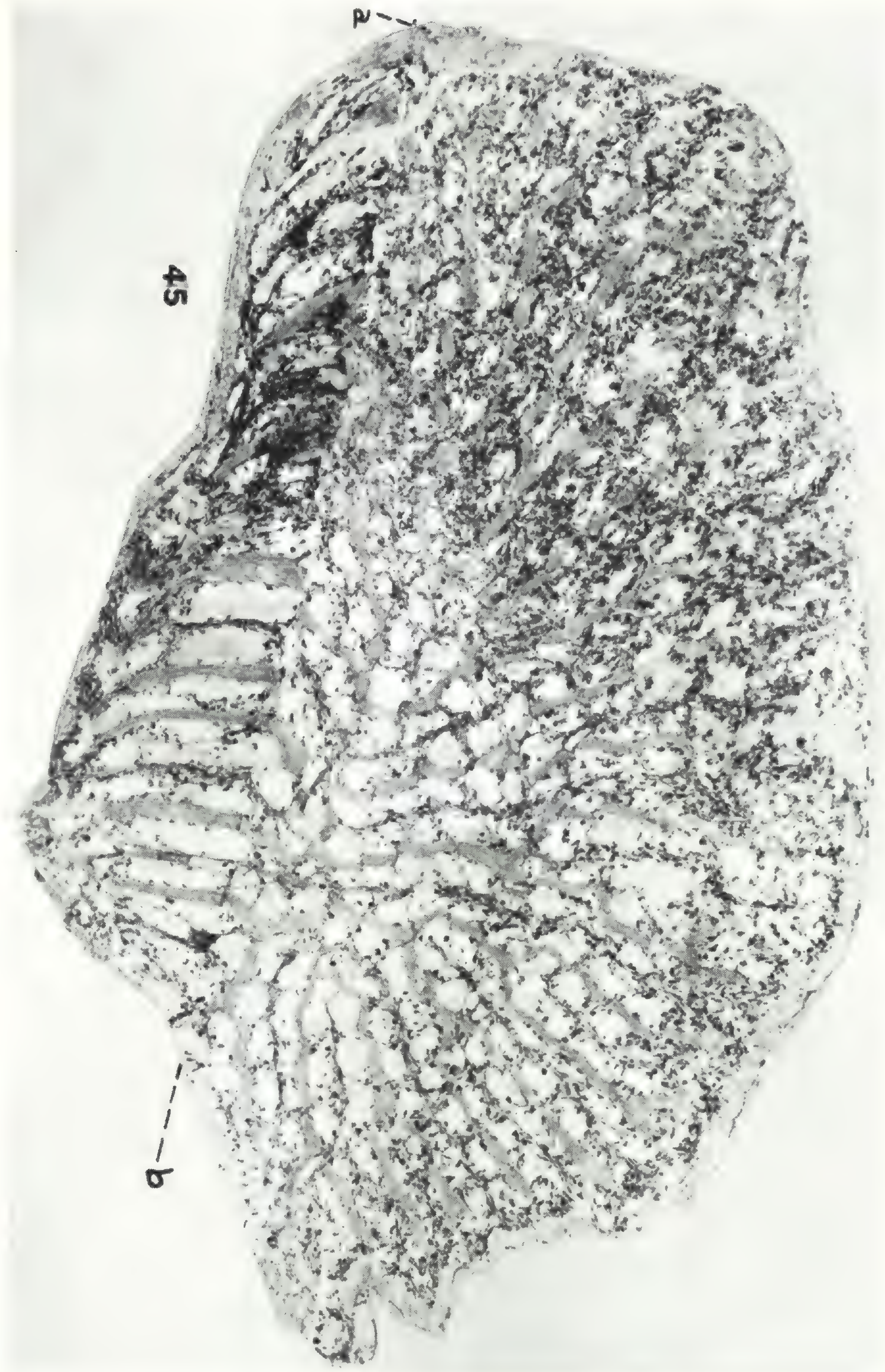

a
b

EXPLANATION OF PLATE

PLATE 14

Dolerotheca sclerotica

Fig. 45. Transverse-longitudinal view of entire fructification. Below the line *a-b* is the longitudinal cut showing the curving of the marginal sporangia; above is the transverse cut showing the bifurcation of the thick sclerotic bands, between which can be seen the parenchymatous-secretory tissue forming the sporangial walls. The upper right-hand margin shows the sclerotic hypodermal zone. For more detailed view see figs. 48 and 49 from slide 1628, × 9.


p
45
a

Explanation of Plate

PLATE 15

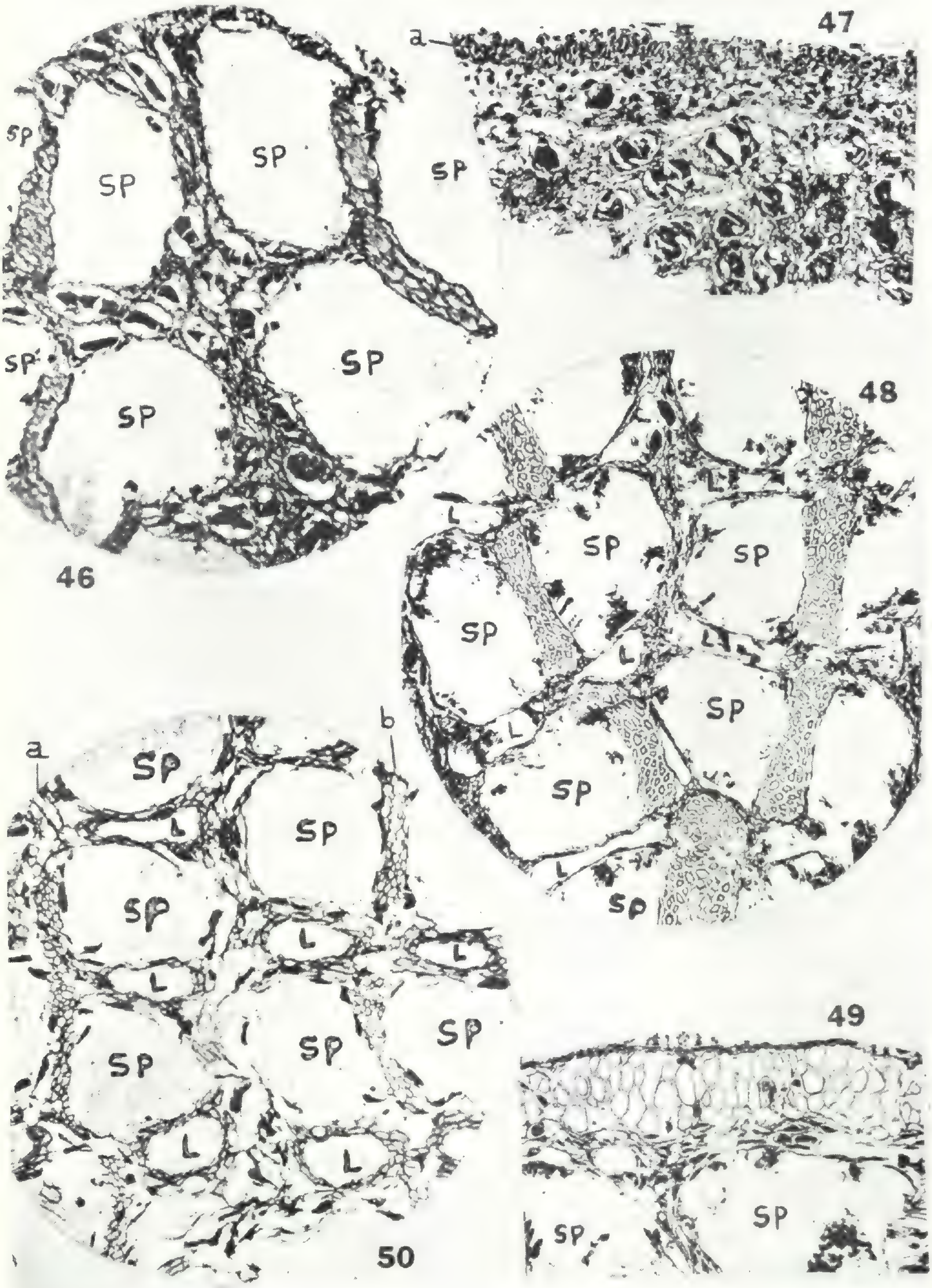
Fig. 46. *Dolerotheca Schopfii.* Transverse view of a double row of tubular sporangia showing four empty sporangia separated by the slime canal and sclerotic ground tissue and enclosed on the left and right by the thick sclerotic bands. Note absence of lysigenous tube between sporangia; *sp*, sporangium. From slide 1629, × 22.

Fig. 47. *Dolerotheca Schopfii.* Transverse view of campanulum wall showing pubescent epidermis and secretory-sclerotic hypodermal zone; *a*, glandular hairs. See fig. 57 for detail of hairs. From slide 1629, × 40.

Fig. 48. *Dolerotheca sclerotica.* Transverse view of a double row of sporangia separated from portions of two other rows by the thick sclerotic bands. Note thin-walled lysigenous tubes alternating radially with the sporangia and bifurcation of the sclerotic bands; *sp*, sporangia; *l*, lysigenous tubes. From slide 1628, × 32.

Fig. 49. *Dolerotheca sclerotica.* Transverse view of campanulum wall showing epidermis and sclerotic hypodermal zone; *sp*, sporangia. From slide 1628, × 40.

Fig. 50. *Dolerotheca formosa* Schopf. Transverse view of a double row of sporangia with the alternating smaller lysigenous tubes. *a* and *b* indicate the much less conspicuous sclerotic bands than in figs. 46 and 48; *sp*, sporangia; *l*, lysigenous tubes. From slide 1627, × 32.



BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

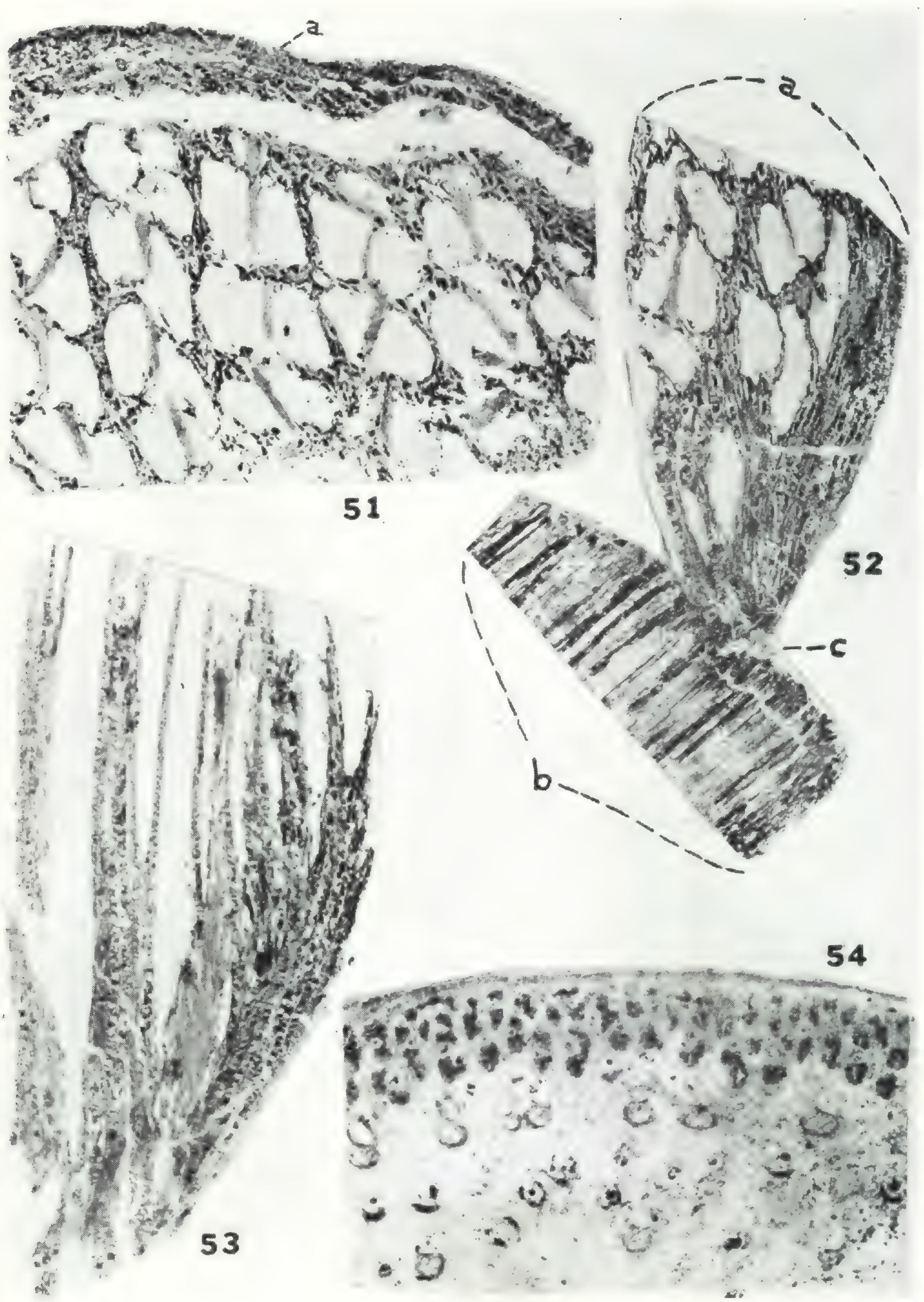
PLATE 16

Fig. 51. *Dolerotheca Schopfii.* Transverse view of marginal portion of campanulum: *a*, broad slime canal and sclerotic zone forming the wall of the fructification partly broken away from inner tissue. See figs. 46 and 47 for detail. From slide 1629, × 8.

Fig. 52. *Dolerotheca Schopfii: a*, oblique-longitudinal view showing possible attachment to *Myleoxylon* sp. at point indicated by *c*; *b*, longitudinal view of hypodermal zone of *Myleoxylon* sp. shown in fig. 54. From slide 1630, × 8.

Fig. 53. *Dolerotheca Schopfii.* Longitudinal view of marginal portion of campanulum showing the ascending origin of the outermost sporangia. From slide 1629, × 8.

Fig. 54. *Myleoxylon* sp. Transverse view of petiole shown in fig. 52b. From slide 1630, × 9.



BAXTER—FOSSIL PTERIDOSPERMS

Explanation of Plate

PLATE 17

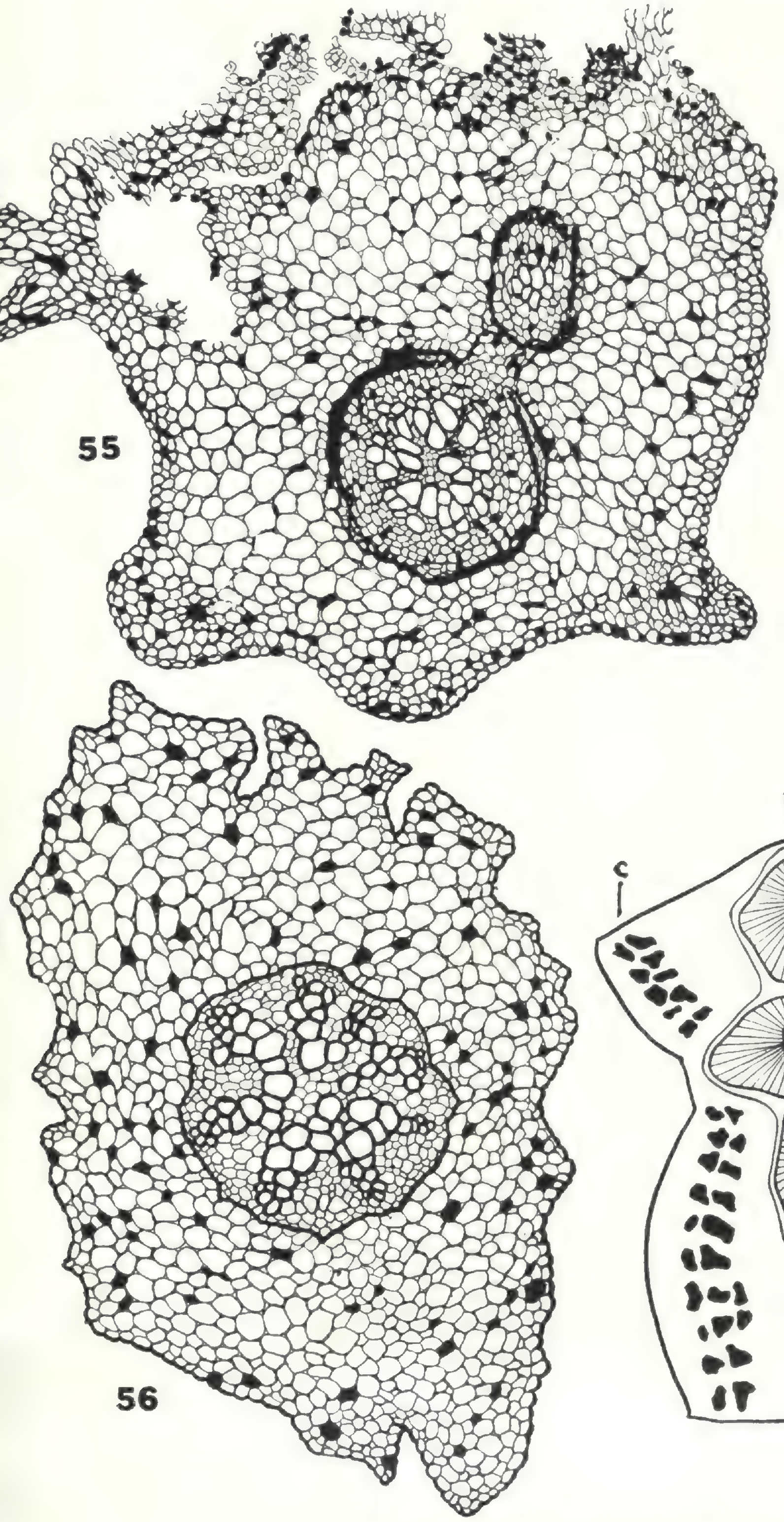
Fig. 55. *Microspermopteris aphyllum.* Cross-section of small stem or branch showing departure of branch bundle. This represents a stage shortly above that shown in fig. 3. From slide 1632, × 26.

Fig. 56. *Microspermopteris aphyllum.* Cross-section of an adventitious root. From slide 1633, × 34.

Fig. 57. *Dolerotheca Schopfii.* Drawing of epidermal hairs. From slide 1629, × 350.

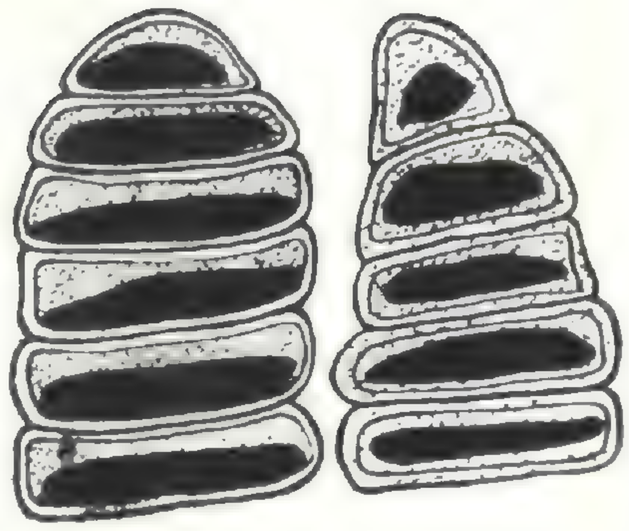
Fig. 58. *Dolerotheca sclerotica.* Drawing of one of the rare glandular epidermal hairs. From slide 1631, × 550.

Fig. 59. *Medullosa Thompsonii.* Diagram of central portion of the stem: *a*, stelar assembly; *b*, line of "aggregate leaf traces" at point just above the departure of a petiole as indicated by absence of hypodermal fiber strands shown at *c*. See fig. 30 for detail of a single "aggregate trace." From slide 1626, × 4.



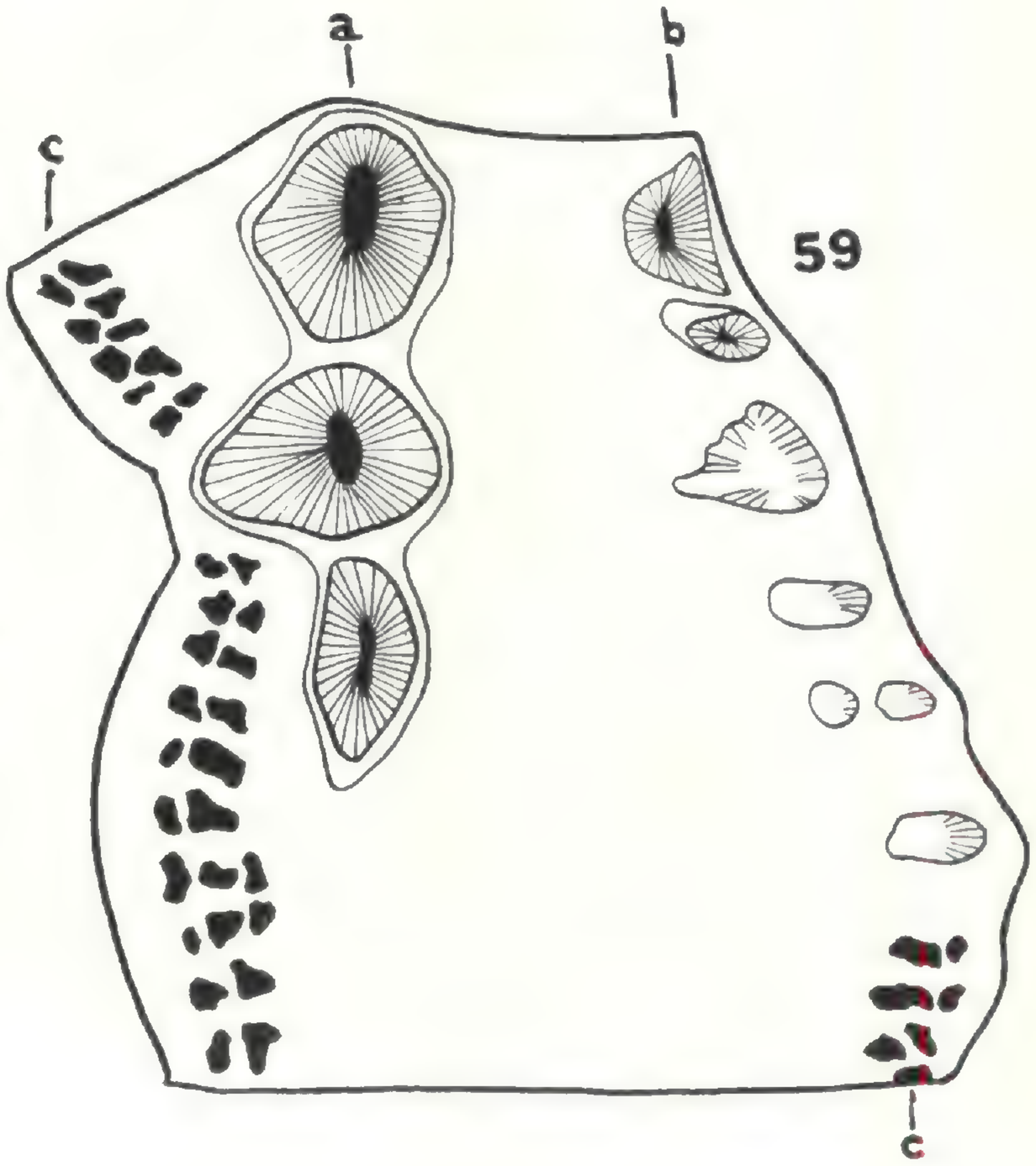
55

56



57

58



59

BAXTER—FOSSIL PTERIDOSPERMS

MAIZE AMONG THE HILL PEOPLES OF ASSAM

C. R. STONOR AND EDGAR ANDERSON

INTRODUCTION

Maize is widely grown in the Orient and is used there for a variety of purposes. Authorities once quite commonly believed that it originated there, but the demonstration that it was almost universal in the New World in pre-Columbian times made an American origin seem most likely. From a meticulous investigation of the historical evidence Laufer (1907) concluded that maize did not reach the Orient until post-Columbian times, and Merrill (1941, 1946) produced convincing evidence that maize and other New World crops had been carried to the Philippines at an early date by the Spaniards and had been widely spread on the continent of Asia. The subject seemed closed and the lack of any evidence for pre-Columbian maize in the Orient became one of the most powerful arguments against any effective trans-Pacific communication in pre-Columbian times.

Several years ago the two authors of this paper came independently to the conclusion that the subject needed to be reopened and examined on its own merits. The senior author, working in the mountains of Assam, found distinctive varieties of maize widely cultivated by the primitive Nagas. The ethnological and linguistic evidence suggested that these varieties had been in that area a very long time and most probably must have arrived there in pre-Columbian times. The junior author, having made a beginning at distinguishing between the various races of *Zea Mays* (1942, 1943, 1946), found that the history of maize in the Orient was apparently complex. There was abundant evidence that Merrill was right and that varieties quite similar to those grown in the Caribbean had been brought to the Philippines and Guam by the Spaniards and have since that time been widely spread and extensively grown in the Orient. However, the popcorns, green corns (i.e. those used as a fresh vegetable) and brewing corns did not fit into this picture at all. Almost without exception they are grown by primitive peoples. Their distribution is notoriously spotty and is mostly confined to various ethnological back corners. The Oriental popcorns, furthermore, are not at all like the popcorns of Central America. They are on the whole similar to varieties of maize grown in Peru and Chile in early prehistoric times. As soon as one was able to distinguish effectively between different races of maize, Laufer's conclusions were no longer valid. His evidence can now only be interpreted as showing that maize in the Orient has had a long and complicated history. At an early date the popcorns, green corns, waxy corns, etc., spread widely in the Orient. At a much later date different varieties of field maize were introduced by the Spaniards, and over wide areas are the only type being grown today.

Through the good offices of Dr. W. B. Turrill and Mr. C. E. Hubbard of the Royal Botanic Gardens at Kew, the two authors were put in touch with each other

and since that time have worked together as closely as the distances involved and disturbed world conditions would permit. The collections of native kinds made by Stonor have been grown, pressed, measured, and photographed in Assam. Samples of the same varieties were grown by Anderson at the California Institute of Technology (through the courtesy of Dr. E. G. Anderson) and were pressed, measured and photographed. Pachytene smears were made of each culture with the assistance of Dr. A. E. Longley and Dr. W. L. Brown.

In the following paper the evidence relating to these Assamese varieties, evidence ethnological, linguistic, distributional, morphological, and cytological, is set out as objectively as possible. Part I was written by Stonor, Part II by Anderson. To the authors the conclusion seems inescapable, that there are at least two races of maize in Asia and that one of these must have crossed the Pacific in pre-Columbian time. The direction (or directions) in which it travelled, however, is still uncertain. This new evidence, in other words, tells us little or nothing about the origin of maize. It does, however, enlarge the possibilities which must be considered in any serious investigation of that fascinating problem.

PART I

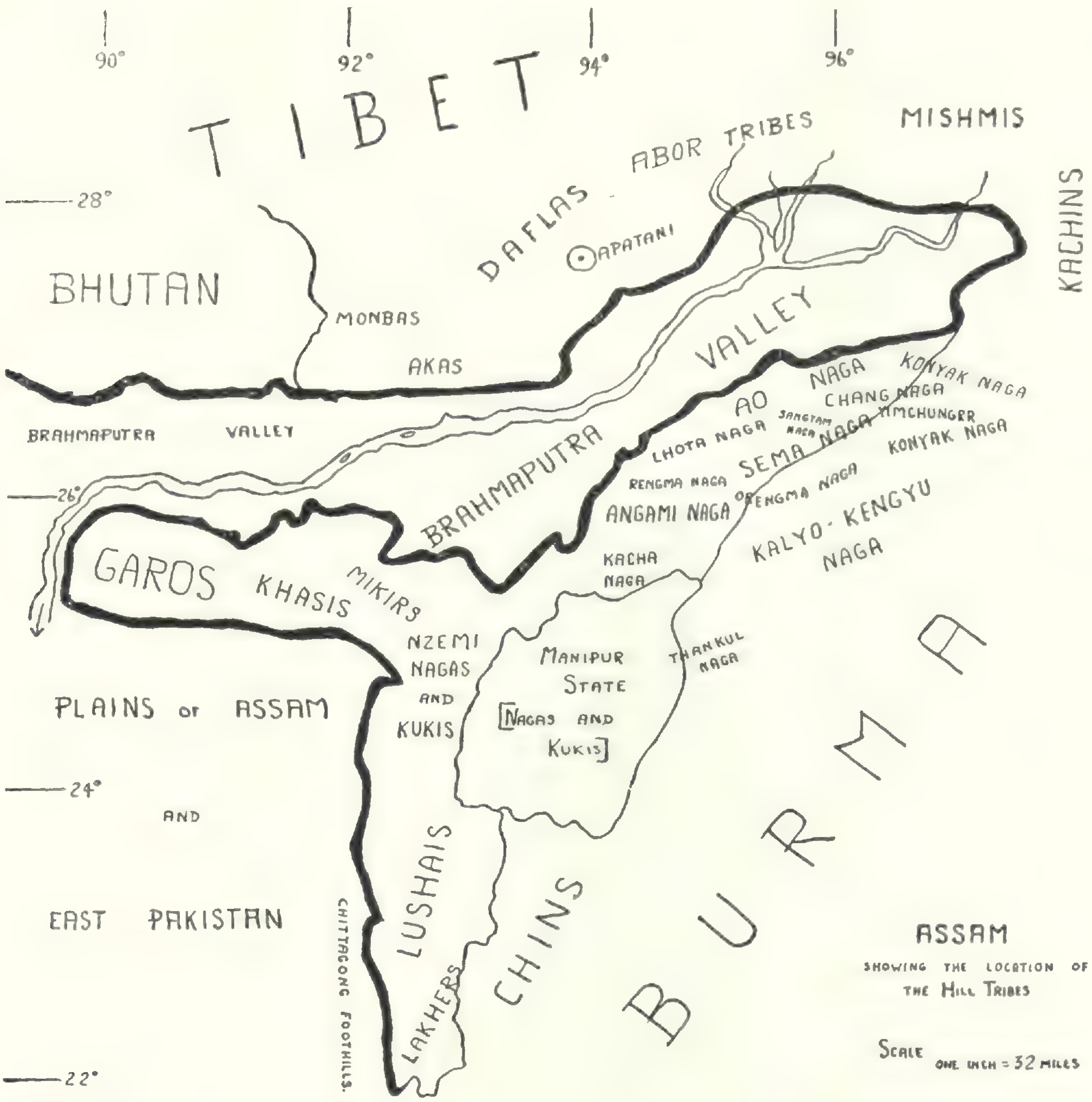
C. R. STONOR

Before detailing the uses of maize among the hill tribes of Assam, it is necessary to give a very short general account of the tribes themselves and particularly from the angle of their probable origins and directions of migration.

Taking first the tribes of the Assam-Burma border:

1. NAGA TRIBES:—The Naga Hills are inhabited by at least ten tribes, who, although they possess a number of features of culture indicative of common elements in their origin, show many sharp differences in culture, language, traditions, temperament, and physical characters. The Naga tribes are, in fact, more correctly described as the tribes inhabiting the Naga Hills. It is well established that they have elements in their culture complexes indicating wide diversity of origin. There are well-established links with Indonesia, Burma (including the Burma-China border), the Pacific and India. The dominant element today is widely different from any of the main cultures of India, and far more bound up with tribal peoples of Indonesia and southeastern Asia (including Burma). It is certain that there has been continuity of settlement in the Naga Hills for many centuries or millenia. Stone celts are commonly found in the hills, although no tribe today has any tradition of ever having used them. There has probably been a good deal of movement to and from the hills from the Brahamaputra Valley.

2. LUSHAI-CHIN-KUKI TRIBES:—These tribes have limited affinities with the Nagas; and their immediate origin seems to be from hill regions of Burma, where they are closely related to the Karens. There are also undoubted kinships with Indonesia. They are pronouncedly Mongolian and have little or nothing in common with any part of India.



3. MANIPUR STATE:—Manipur State is inhabited by a hill population of mixed Kuki and Naga elements, and the big population of the great valley of Manipur is partly derived from these (and particularly the Nagas), and partly from an ancient Mongolian element of uncertain origin.

Taking the tribes of the ranges running east and west and bordering the Brahamaputra Valley on the South in Assam:

1. MIKIR TRIBES:—The Mikir Hills are inhabited by mixed tribes of uncertain origin. There are probably links with both Kukis and Nagas and with the peoples on all sides of them.

2. KHASI TRIBES:—These are classed with the Mon-Khmer group, and their main origin is generally regarded as being the region of Indo-China. It is quite possible that there is an ancient strain in the population akin to the aboriginal stocks of peninsular India and originating from further West. The Khasis are widely different in many respects from the other tribes of Assam.

3. GARO TRIBES:—The Garo tribes have definite affinities with elements among the Nagas and with tribal peoples of the Plains of Assam. There is also some indication of links with Bhutan, and there may well be kinship with parts of India to the West.

Turning to the tribes of the Assam Himalayas lying north of the Brahamaputra:

4. MISHMI, ABOR, APA TANI, DAFLA AKA, MONBA and LAMAI:—The tribes of the Assam Himalayas, divided extremely roughly into Mishmi, Abor, Dafla, Apa Tani, Aka, Monba and Lamai as the main groups, have been very little studied. There has undoubtedly been much migration from the east and I am of the opinion that a big element in the population is akin to the Kachin peoples of northern Burma. There are marked cultural similarities with the Naga tribes, mainly among the Abors. There has been infiltration down river valleys from Tibet and very possibly in the reverse direction into the hills from the Brahamaputra Valley. The Monbas, a small tribe living near the Bhutan border, may have originated from that state.

Even these meagre notes show the hill tribes of Assam to be as mixed a population as can well be imagined, who are linked with literally every part of Asia. Prehistoric (?) stone celts are found throughout the hills, indicating very ancient population. These celts are recorded in the literature from all hill areas south of the Brahamaputra, and I have celts in my possession from the Abor and Dafla Hills of the Outer Himalayas.

Except for the Angami Nagas, the Apa Tanis and the Monbas, and to some extent the Khasis, the basis of subsistence economy is still dry cultivation, carried out by cutting and burning the forest and raising crops for one or more seasons in the area so cleared. The main subsistence crop in the majority of cases is rice, but millets, Job's Tears, sorghum, maize, are all important and are grown in varying amounts by nearly all tribes. In a few instances, one or other of these cereals is as important as rice, as, for example, among the Abor tribes, who grow rice and Job's Tears in almost equal amounts, or the Chin tribes of Burma and the Monba tribe of the Bhutan Border, who grow more maize than they do rice. It seems probable that the complex of Job's Tears-millets-maize preceded rice as the main food supply of many tribes.

In general, the tribal peoples of the Assam mountain tracts live in the so-called Neolithic stage of culture. The community is a self-contained one, growing its own food, weaving its own cloth, regulating its own affairs by tribal law. There is no writing, and the religion is animistic. The level of culture is very similar to the tribes of Borneo, the mountain tribes of the Philippines, and some at least of

the South American Indians. In the Naga, Lushai, Khasi, Mikir and Garo hills there has been missionary activity for some decades, and the tribes have been administered for the same period, so that far-reaching changes have set in. This is not, however, of consequence for my present purpose, the more so since administration has done remarkably little to change or to develop the economic life. In the Himalayan tracts north of the Brahamaputra, administration has only been started since the end of the War. Missions are banned from entry, and large tracts are still unexplored.

DETAILS OF VARIETIES, CULTIVATION, USE, ETC., OF MAIZE AMONG THE HILL TRIBES OF ASSAM

The notes which follow are all based on information obtained at first hand in the field, either by direct observation or questioning members of the tribes concerned, or more usually by a combination of both. Where I have had to rely on the work of others, or have not visited an area, I have drawn attention to the fact.

1. ANGAMI NAGAS:—

Varieties grown: Nos. 5–18, particularly the larger flint types.

Ecology and technique: The Angami Tribe lives in hills from 2500 to over 6000 feet in altitude. The great bulk of the tribe lives above the 4000 feet level and in a sub-temperate climate. Maize is universally grown, and the larger flint types predominate. The Angamis have a remarkable system of irrigated rice-cultivation, and only a small proportion of their crops is grown on dry fields. Maize is grown mixed either with millet and Job's-tears or else as a pure crop, usually in small plots in the immediate vicinity of the village. Sowing is by dibbling.

Uses: Their irrigated rice-cultivation leaves the tribe well provided for. Maize, along with millets and Job's-tears, is important for human consumption mainly among poorer people who are short of rice fields. It is, together with subsidiary crops (notably millets), a catch-crop to "fill up corners" before the rice is harvested. It is eaten fresh, either boiled or slightly roasted, and is largely consumed by children. The main use among this tribe, in years of good harvests at least, is for *pig feed,* the grain being parboiled and roughly mashed. It is only so used when actually in season, and is not stored for feeding the pigs. Small quantities of the popcorn types are stored for popping, but this is not important. It is used occasionally as an ingredient in beer, along with other cereals.

Storage: The ears are hung up on the rafters of the dwelling house for next season's seed.

Folklore, traditions, etc.: The Angamis I have talked to simply state that they have grown maize from time immemorial. The tribal name of corn is *Tsüke.*

2. LHOTA NAGAS:—

Varieties grown: The varieties grown in the village of Yimbang at elevations of less than 2000 feet in the sub-tropical lower ranges of the area are:

1. *Tchetum-sopfu* (Serial L. 1), meaning "Small late," regarded as an indigenous variety.

2. *Moro* (Serial L. 2), meaning "Quick or early eating," regarded as indigenous.
3. *Aorr-chemyang* (Serial No. 6 of first consignment), meaning "Ao Nagas blood." This refers to traditional origin from the neighbouring Nagas, the term blood having reference both to the small red grains, and to the former enmity between Lhotas and Ao's.
4. *Konoma-tsunghundhro* (Serial No. 8 of first consignment), meaning "Konoma Maize," the name Konoma being that of a large Angami Naga village to the south of the Lhota country, and indicating that it probably derived from there. A very similar type is known as *Wokotsu*, because it was first got by Yimbang from a Lhota village of that name.
5. *Epuk* (Serial No. 12 of the first consignment), meaning "Bursting," as it is only grown for popcorn.
6. *Kor-chak*, meaning "Horse-Food." This variety, a coarse flint maize grown in many parts of India, was obtained within living memory from Nepalese immigrants into this region. The name is derived from the custom of the Nepalese of keeping ponies.

The main varieties grown in the village of Yekhum, in the higher areas of the Lhota country and almost within sight of Yimbang, where conditions are between sub-tropical and sub-temperate and the altitude about 4,000 feet, are only two: (1) *Korchak* and (2) *Konoma-tsunghundhro*. Both are said to be of fairly recent introduction, and supplanted other types. Other types may be grown in small amounts.

Ecology and technique: A great part of the Lhota Naga country is sub-tropical, and there are few villages situated over 4,000 feet. The types grown are naturally those most suited to this climate. Maize is grown as a mixed crop among the rice and subsidiary cereals. It is commonly sown in rows along the edges of field paths or inter-field boundaries. The seed is dibbled, and the sowing season is March–April, while the harvest is from June to early August.

Uses: Maize is not a very important crop among the Lhota Nagas and, as among the Angamis, it is grown wholly as a catch-crop, utilized before the rice harvest is in. But it is grown entirely for human consumption, and except for the popcorn *Epuk* variety, it is entirely consumed as it ripens. A little is used now and again for beer-making. The reasons for growing the different types is gone into in more detail below.

Storage: The ears for next season's seed are simply hung up on the rafters of the dwelling house.

Traditions, folklore, etc.: The general word for maize is *Tsunghundhro*, which means "something obtained from the Angami Nagas," and I have been told of a vague tradition that the Lhotas first got maize from their Angami neighbours. On the other hand, the variety *Tchetum-sopfu*, listed above, is regarded by the Lhotas as their own maize and does not seem to be grown by the Angamis.

The Lhotas have been in their present country for a matter of centuries. They state that they have had maize from time immemorial.

3. AO NAGAS:—

Varieties grown: Some or all of Serial Nos. 5–18.

Ecology and technique: Closely parallels that of the Lhota tribe.

Uses: As among the Lhotas, it is entirely for human consumption.

Storage: As for the Lhotas.

Traditions, folklore, etc.: The Ao Nagas have a tradition that they have always grown maize among their field crops. The usual name for maize is *Mentia*, for which I can get no translation. A small group of villages which have a different language know it as *Achang-Tangba*, which means "bearing rice already husked." A curious local name has been recorded by J. P. Mills ("The Ao Nagas," 1926. p. 125, footnote) as used in the Ao village of Changtongia: *Moya zungkhum*, meaning "Sema Naga Lentils."

4. SEMA NAGAS:—

Varieties grown: Some or all of Nos. 5–18.

Ecology, technique, etc.: Very much as for the Lhotas and Ao's, except that maize is a much more important crop and is planted thicker on the ground. Sown during March–April, and harvested in June–August.

Uses: Is of considerable importance for human consumption, both fresh on the ear and (to a lesser extent) stored and pounded to mix with rice. It is also used to make several types of strong beer, again to a greater extent than among other Naga tribes. My information from the Sema area is scanty. However, the importance of maize is very likely linked with the shortage of land for cultivation and the large population of poor people, so that the staple food of rice is apt to be finished well before the next harvest. Catch-crops are consequently of much importance, and rice insufficient for beer-making.

Traditions, folklore, etc.: The Semas regard maize as an ancient crop. The name for it is *Kolakithi*. This is usually translated as "Foreigner's Job's-tears," and some Europeans have assumed without evidence "Foreigners" to mean the British and that maize was introduced into the Naga Hills by the British (!). Apart from this, I have been given another meaning for the word by a Sema Naga: "Grain that is eaten by plucking singly." Another word is *Amehukethi*, meaning "a grain ripe and eaten before the rice."

5. CHANG NAGAS:—

Varieties grown: Some of Nos. 5–18.

Ecology, technique, etc.: As for other Naga tribes. Most of the Chang Naga country is high and cold with sub-temperate climate, and the larger coarser flint types predominate. A small popcorn (Serial No. 12) is grown, and the African dent maize is also cultivated.

Uses: Except in a few low-elevation villages, the Chang Nagas even today depend largely for their subsistence on millets, Job's-tears, maize and taro, rather than rice. Maize is thus an important crop. It is, however, largely a catch-crop, eaten fresh, but appreciable quantities are stored and are mixed with other cereals for food during the cold weather. It is used preferably in making beer, and to a small extent for popcorn. Some, particularly in seasons of good harvest, is fed to the pigs.

Storage: In round baskets, stripped from the cob, in separate granaries.

Traditions, folklore, etc.: The Chang name for Maize is *Hangi,* for which I can get no translation. It is certain from their traditions and recent history that the Chang Nagas have been pushing west from the Burma side for some generations, and they themselves claim that at least a large element in their composition came from further east. Their economy is as noted, still based very much on Job's-Tears, millets, and maize. This is partly due to their living largely in high altitudes and possessing no suitable type of rice for the climate; but I have several times been informed by Changs that it is only since they have had contact with the more westerly Naga Tribes that they have taken to rice at all; and rice is widely recognized as being a more recent crop than the other cereals, maize not excluded. Among this tribe each major crop has its own minor tutelary deity, maize among the rest. The African dent maize is known as *Bilati Hangi,* meaning "English Maize."

6. YIMCHUNGRR, KONYAK and KALYO-KENGYU NAGAS:—

I have very little information from any of these tribes. Maize is grown in varying amounts by them all. It is said to be an important crop among the Kalyo-Kengyu, but not very much grown among the Konyak Nagas, who are among the most ancient stock in these hills. I have visited the extreme northeast area of the Konyak country, where a poor type of one of the larger-grained flint maizes is grown in small quantities. I was told that the people were not keen on it as it attracted bears to the fields. The Konyak name for maize is *Tongi.*

7. KACHA NAGAS and NZEMI NAGAS:—

These two closely allied groups inhabit the southern Naga Hills. I have been there once and can confirm that maize is grown in the fields along with other cereals, and my original stock of small-grained types came from this area. The area varies a great deal in elevation (from 1,000 to 7,000 feet) and most or all of Nos. 5–18 are grown.

I have a rather vague report from a Government subordinate concerning a branch of the tribe living in the hotter areas, about 3,000 feet, that three main types are recognized: (1) *Imbaume mei Mitak,* early; (2) *Lingtak,* second to ripen; (3) *Lingtak tiingne,* late. The first two are said to be the most widely grown.

The Kacha Nagas have a tradition that the tribe first emerged from a cave in their area, and brought their old established crops with them, maize being among them. I have no details of its use except that most or all the crop is used as it ripens and is not normally stored.

8. SANGTAM NAGAS:—

There are two geographically separated branches of this small tribe. I have visited the northern branch.

Varieties grown: I have obtained the following list and notes from a Government subordinate, himself a member of the tribe.

1. *Chemese*, sown in March and harvested June to July.
2. *Mesease*, meaning "sweet maize." Is regarded as good for making beer and is grown mostly in rocky fields.
3. *Nurachese*, a small popcorn maize.
4. *Hengchimerem*, used both for human consumption and for pig feed.
5. *Yengchengese*, used mainly for beer and for pig feed.
6. *Ahochese*, not regarded as very good, but grown as it is ripe earlier than the rest.

Unfortunately, my small collection from the northern Sangtam area got rather mixed and labels lost. I can, however, note that of the above No. 2 is a small red-grained type similar to but larger than Serial 6. No. 2 *(Mesease)* is a very small white-grained popcorn identical with Serial 12. No. 4 *(Hengchimerem)* is a fair-sized maize with large, coarse grains, and a proportion at least are red. No. 6 *(Ahochese)* is a stout rather coarse type with large hard yellowish-white grains.

Ecology, technique: The northern Sangtams live in steep country, and grow their maize mixed with millet in their ordinary fields.

Use: The above list shows the main use of maize and I have little to add. Most is said to be eaten when soft, but a proportion is stored for the winter, when its main use, except in seasons of rice shortage, is for beer. It is a fairly important catch-crop, probably more so than among the Ao and Lhota Nagas. Much of the Sangtam area (as among the Chang Nagas) is high and cold and unsuited for rice growing.

Storage: In baskets, after shelling, in the granary.

Folklore, traditions, etc.: The Sangtams simply informed me that they have always had maize among their crops, as far back as their traditions reach.

9. RENGMA NAGAS:—

I have never visited this little tribe, which is split into two geographically separated parts, of which the eastern branch is very primitive. Writing of the eastern Rengmas, J. P. Mills ("The Rengma Nagas," 1937, p. 86) states:

> On the *jhum* maize is a far more important crop than it is in the Western Rengma country. It is both eaten boiled and used for brewing. Ordinarily it is sown scattered among the Millet *(achota,* the *Sorghum)* with which it is harvested, but some men grow whole fields of it.

Of the western branch of the tribe, the same writer says (l.c., p. 77): "Maize —though an important crop among the Eastern Rengmas, is little grown by the Western Rengmas. At most a few plants are grown among the rice and the heads roasted and given to children to eat. Occasionally a brew is made from it nowadays, but the resulting beer is not popular." The words for maize are (both from Mills): Western Rengma—*Samphuruchi,* and in Eastern Rengma—*Akhuzi.*

Mr. Mills has recorded from the Eastern Rengmas (p. 88):

> Early in August there is a series of five "genna" days. The first day is called *Atsetatsate,* and is held to prevent waste of food. The next four are called *Tsate,* the festival of formal first fruits, that marks the beginning of the maize and millet harvest. Young men go to the fields and bring back leaves of millet, which only the women eat, or pretend to eat raw. Men also bring in Maize-heads that day. These are not eaten that day, but kept till the next day but one following, when everyone eats roasted Maize. Throughout this "genna" all work ceases and people entertain their friends at drinking parties.

10. THE LUSHAIS:—

Varieties grown: L1–L8 as sent. A list of the types grown, as sent me by a reliable government subordinate is:

1. *Ralte Vaimin* (Serial L1), regarded as indigenous.
2. *Pawi Vaimin* (Serial L5), meaning "Chin Maize."
3. *Sap Vaimin,* meaning "European Maize." This variety is a dented maize recently introduced by the British.
4. *Bawngpu Vaimin* (Serial L7), meaning "Herdsmen's Maize." This is a large coarse flint maize introduced by Nepalese immigrants (the "Herdsmen").
5. *Chingzo,* meaning not given.
6. *Vai Vaimim* (Serial L4), meaning not given.
7. *Lenliam* (Serial L6), meaning not given.

   Nos. 5, 6, and 7 are regarded as similar, and have small, dark-grained ears noted for the stickiness of the grain while soft.
8. *Puakzo* (Serial No. L8), meaning "Burst all," as it is grown for use as popcorn.

Ecology and technique: I have not visited the Lushai Hills, but have first-hand information that, as among the Nagas, maize is grown among the other crops in the dry *jhum* fields, and occasionally as a pure crop. In the latter case I am informed that it is usually followed by a legume crop. The seed is dibbled, and the sowing season is said to begin in April, with the harvest from July to August.

Uses: The bulk of the crop is eaten, boiled or roasted, as it ripens, and is thus a catch-crop as among the Naga tribes. It is also used to some extent as pig food, and a little fed to poultry. Limited amounts are stored (presumably by poorer people, and in lean years), and the grain is roughly pounded and mixed with rice. The small *Puakzo* is probably grown entirely for popcorn. I have no information of maize being used for beer, and I think it to be so used very seldom. Some of the

Lushais in the high-altitude eastern areas with a cold climate use maize as a main crop; this is due to lack of a high-level rice, and will be described under the Chin tribe.

Storage: I have no information.

Traditions, folklore, etc.: Lt. Col. J. Shakespear ("The Lushai Kuki Clans," 1912, p. 87) states that there is a festival known as *Mim-Kut*, named after the Maize, as it takes place when the crop ripens. It is of but little importance and seems likely to die out. Cakes of Job's-tears are eaten, and the next day is *hrilh*. N. E. Parry ("A Monograph on Lushai Customs & Ceremonies," 1928, p. 91) refers to this feast as being in honor of persons who have died during the past year. He mentions that the "Fresh vegetables, maize, bread, necklaces, & cloths are placed on the memorials of the dead."

Shakspeare remarks of the chiefly clan of Fanai, who originated from the Chin country to the East (l.c., p. 139): "A dead Fanai is buried in the usual Lushai way, but no rice is placed in the grave. An offering of Maize is however suspended above it. It may be noted that in the Zahao country rice is not cultivated, the staple crop being maize."

It is possibly an exaggeration that maize is the only main crop in this area: but I have had it confirmed by members of the Lushai tribe that it is more important than rice.

11. THE LAKHERS:—

I have not visited this tribe, which lives next to the South Lushais. Their system of cultivation is the same as among the Lushais, and it is reasonably certain that maize is grown in the same way, and is of the same importance. The Lakher word for Maize is *Chhamei*. Rice is the staple crop. A minor use of the dry grain is mentioned by Mr. N. E. Parry ("The Lakhers," 1932, p. 199), who states that it is used for counting. The same authority describes a very interesting dance performed in one village in connection with the maize harvest (l.c., p. 434):

> In Chapi village, to celebrate the gathering in of the Maize harvest, a dance called *Pazutawla* is performed. The men hold hands and form a ring; the girls stand in front of them; one girl stands between two men, and puts an arm around the shoulders of the men on each side of her. They dance round and round, singing to the accompaniment of gongs and drums. The dance is peculiar to Chapi. It is *ana*, to dance it except in celebration of the maize harvest, and were it performed at any other time those taking part would suffer from carbuncles.

12. THE CHINS:—

In the Chin Hills, which are politically within the borders of Burma, maize is a very major crop. All my information is from "The Economics of the Central Chin Tribes," by H. N. C. Stevenson (1943).

Stevenson lists maize as among the staple crops (p. 35) and states that it is grown along with millets and beans. The system of cultivation is as a mixed crop in the *jhum* fields. The ears are stored, hung from the rafters of the dwelling-house. He implies that it is of equal importance with rice. It seems to be used

both fresh and after being stored; it is used, mixed with rice and millet, for beer-making.

Stevenson gives interesting notes on uses of stored maize. Thus under "Travel Rations," which he describes as being the most common form of cooked food in pre-annexation days, owing to constant danger of raids, he includes . . .: *Vainiim kan*.—"As the name implies, this is roasted maize, and it is prepared in exactly the same way as *Vai kan*. Occasionally, when it is to be eaten the same day, bananas are pounded into the grain as a change of flavour."

He describes the *Vai kan* just referred to as follows:

> The name means roasted millet, *faang klawr* again being the variety used. The grain is soaked in water for a minute or two to damp it thoroughly and is then steamed as if to prepare it for fermenting, after which it is spread on mats to dry in the sun. In the final stages of preparation the swollen grain is roasted in a *peibung* until it bursts like puffed wheat. The whole is then pounded with salt or honey and made into convenient lumps which are taken on hunting parties, etc. *Vai kan* is regarded as best of all foods for "sticking to the ribs" but it is very dry, especially the salted variety, and for this reason is not used during hot weather in areas where water is scarce . . . . . .The *peibung* is the traditional grain-roasted pot, shaped rather like a beer-pot, but with a large hole in one side. Its very existence proves the antiquity of the roasting method of cooking.

The same authority lists under the heading "Daily food in the home":

> *Thiah Var:*
> This is the commonest food of the present day, and it is generally made with maize, millet being reserved for beer-preparation or the travel ration. The maize is pounded to break the grains and then sieved and boiled in water. It is eaten with any sauce that is going, after the liquid has been drained off. When consumed as a broth with the water in which it is cooked it is called *ti sawp*, and if pumpkin and other leaves are added as a flavoring it becomes *buh ber*.

The harvest is apparently later than in most of the Assam Hills, presumably for climatic reasons. Stevenson states (l.c., p. 41):

> No sooner is the millet crop safely gathered than the maize ripens in August and September. In harvesting maize also the Chin use no knife but tear the cobs off by hand, removing the outer cover and turning the inner ones back to act as ties when the cobs are eventually stored under the rafters of the house.

With regard to the use of maize for beer-making, Stevenson records (l.c., p. 113):

> In the Central Chin Hills there are three recognized types of beer: *zu ha*, made from first-quality cleaned millet; *zu pi*, made of husked millet mixed with its chaff; and *vainiim zu*, made from Maize . . . . . [*vainiim zu*] is made of pounded Maize, which after being soaked for a day to soften is treated like the millet used for *zu ha*. Like *zu ha*, it will not keep for long and is therefore prepared shortly before use. This *zu* being the cheapest, is most often used in the home on day-to-day occasions.

Maize seems to be too important for human consumption to be given directly to domestic animals. Stevenson notes, however (p. 114): "Incidentally, fermentation of grain for beer does not waste the solid residue: this by-product is added to the pig-food and gives strength and substance to the unappetizing bulk of banana stalk which is the other main ingredient." As a corollary to this, I may add that this use of the fermented grain of millet, rice, maize, etc., for feeding pigs is a

universal practice among all the Nagas and other tribes.

The Chin word for Maize is *Vainiim*.

13. THE KUKIS:—

The Kukis live in the Southern Naga Hills, and in Manipur State. I have once visited a few Kuki villages in the former area, among whom maize was grown and used in precisely the same manner as among their Naga neighbors: as a catch-crop for consumption while fresh, for popcorn, and to a small extent for beer-making. The same types are grown. The name for Maize among the Thadou branch of the tribe is *Kolbu*, which is said to mean "Burma Food": an interesting point since the Thadou Kukis are generally regarded as having close kinship with Northern Burma.

14. THE MIKIRS:—

The Mikir tribes have been very little studied. Their system of shifting cultivation is very primitive. Maize is among their subsidiary crops. I have been told by a member of the tribe that the large-grained types are most grown, but the small types are also used. The Mikir word for maize is *Thengthe*. I have not been into the Mikir Hills.

15. THE KHASIS:—

Varieties grown: The Khasis have for generations been in close contact with the British, Nepalese and Indians, and Asiatic, African and American varieties have been introduced and are by now inextricably mixed with older types. Most of the tribe cultivates at over 4,000 feet, and it is doubtful if the small-grained types were ever used to any extent.

Ecology and technique: As a mixed crop, together with rice, millet and Job's-tears. Nowadays the Khasis have a large-scale potato-growing industry, and maize is often grown in the potato plots, interspersed between the rows of potatoes. It is also grown as a pure crop.

Uses: The original uses were for food, mainly as a catch-crop, the ears being eaten boiled or roasted. Some is put aside for popcorn, and in parts of the area it is prepared by placing the grain, with some sand, in the cooking-pot, and heating it over a fire. Maize is become a fairly important cash crop for sale in the bazaar at Shillong. It is used to some extent as pig food.

Storage: Very little is stored, except for seed. The ripe ears are hung up in the house.

Traditions, folklore, etc.: The Khasis state that maize is among their ancient crops. The word for it is *Riew Hadem*, meaning "Grain of the Hadem People." The Hadems are a small branch of the Kuki tribes who live in close contact with the Khasis in the extreme southeast of their area.

16. THE GAROS:—

Varieties grown: G1–G5.

Ecology and technique: The seed is dibbled in lines among the rice and other crops in the *jhum* fields. It is sown about March in most parts and harvested in

June. In some of the warmer areas it is often planted earlier, and I have seen plants with the ear already formed in April.

Uses: Although the staple crop of the Garos is rice, they are hard-pressed for land and food is often short. Maize is an important catch-crop, and is almost entirely used as it ripens. The fresh ears are either boiled or roasted. Very little is stored, and this stored grain is pounded and eaten boiled, either alone or with rice. The smallest variety grown is used only for popcorn, and is prepared by heating it in a cooking-pot with a little sand. Maize is too precious for human consumption ever to be used as pig food; and is said not to be used for beer, which is made entirely from rice.

Storage: When stored for winter use, it is stripped from the ear and put in round baskets. Stock for seed is hung up in the dwelling-house.

Traditions, folklore, etc.: The Garos say they have always grown maize, and got it with their main crops "out of the ground."

* * *

All the foregoing tribes live south of the Brahamaputra, which has always been an effective, but by no means absolute, barrier to contacts of culture. The notes which follow describe the cultivation and uses of maize among the tribes of the outer Himalayas, within the political boundaries of Assam.

17. THE DAFLAS:—

Varieties grown: Serial Nos. 1–4.

Ecology and technique: Maize is grown as a mixed crop along with rice and millets, under the same system as among the Naga tribes. It is the earliest crop sown, and is often dibbled in before the rice, the usual month being March, although I have seen fields sown in February.

Uses: Rice is the staple food among this large tribe, but their technique of shifting cultivation is slovenly and haphazard, and probably for this reason, subsidiary cereal crops of millet and maize are of considerable importance to supplement the rice supply. Maize is both grown more than among the Naga tribes, and much more, perhaps most of the crop, is stored for winter use. I have not been to the Dafla country while the maize was ripening, and cannot say to what extent it is eaten fresh and functions as a catch-crop. However, in normal seasons, it is a subsidiary crop to help out the rice in the winter rather than a catch-crop for immediate use. In the summer following a poor harvest, the people would, of course, be forced to use their maize as soon as it was developed enough to eat. The main use of the stored maize is for food, since the grain is more easily broken up and mixed with rice. For this reason, the smaller-grained of the main types is preferred since the grain is more easily broken up by the pestle-and-mortar grain-pounders. Sometimes it is crudely milled between flat stones. A proportion of the maize is mixed with millet (Eastern Daflas) or with rice (Western Daflas) for beer-making. In good seasons it is used for pig food. Even the dried ears are

often roasted and eaten off the cob. I have several times seen them given to children as "snacks" between meals. All types are used for popcorn. For some years past, Daflas living fairly near the Plains of Assam have carried on a small trade in maize with tea-garden coolies. The Daflas grow only the larger-grained types, and have far fewer types, partially accounted for by the different status of the crop since the large-grained types are clearly more economical for storage than are the small-grained. Climatic factors may, however, enter into it, and it is also perfectly possible that the Daflas have never had the smaller types as grown on the Assam-Burma border.

Storage: Maize is stored in the granary along with other grains. Among the eastern (and more primitive) section of the tribe it is kept on the cob, and the ears are heaped up in a roughly-made rectangular bin in one corner. The western Daflas strip the grain from the cob and store it in large round baskets, usually with the cobs wedged over the top as a protection against rats.

Traditions, folklore, etc.: I have several times questioned Daflas on this. They simply state that they have always grown maize. The Dafla word for maize is *Topothe.* The smaller type grown (Serial 4) is known as *Nyamatup.*

18. THE ABOR TRIBES:—

I have only visited the Padam and Minyong Abors. The other main tribe are the Galong Abors, whose country is adjacent to the Daflas and who are probably very closely related to them. The following note deals only with the Minyong and Padam Tribes.

Varieties grown: Nos. 1–4 (of first consignment).

Ecology and technique: The Abors grow their maize as do all other shifting cultivators as a mixed crop among their rice and millet. They are, however, unique in that they practice double cropping. The first crop is sown during the month of February and is harvested in June. As soon as it is ripe, a second sowing is made in the same field, and is harvested in October.

Uses: The first crop of maize is used purely as a catch-crop, and is eaten while the ears are soft, either boiled or roasted. The second crop is left standing until the ears are thoroughly ripe and the grain hardened off. It is then stored and used during the winter either as a food or for making beer. The proportion that goes for beer-making or for food is said to vary with the economic position of the household and the general abundance of the crops in any one year. In general, maize is an important crop, although rice, Job's-tears, and millet are the staple foods. It is used to some extent for pig feed. Popcorn is also made, but not to any extent.

Methods of Storage: The grain from the second sowing is stored, stripped from the ear, in round baskets in the granary.

Folklore, traditions, etc.: The Abor tribes simply state that they have always had maize among their crops. Their folklore credits them with having obtained

all the main crops "On the horns of the tame Bison," and I have been told specifically that maize is included. The name among the Minyong and Padam sections of the tribe is *Sepa*. The main type used (a large golden or red flint maize) is called *Pade-Pasing Sepa*.

19. AKA TRIBE:—

I have not visited this small tribe, but I have met and talked with several members of it. They all told me that their most important crop is maize, which is grown in their fields along with dry rice. According to my informants, the Aka tribe originated in the Assam Valley, whence they were driven up into the hills many generations ago. At that time their main (or only) crop was rice, and they learned to use maize from the Monba tribe immediately to their west. They informed me that they grow the same varieties as the Monba tribe. The average altitude of cultivation in the Aka Hills is of the order of 5,000 feet.

20. MONBA TRIBE:—

Varieties grown:

1. *Phentang*. Serial Nos. 1 & 2 of first consignment.
2. *Num Phentang*. Serial No. M1.
3. *Khana Phentang*.

The first two are indigenous: the *Khana* is a South African dentate maize introduced a few years back by the government. *Khana* means tooth.

Ecology and technique: The Monbas differ from all other tribes of the Assam Hills in that they are a civilized people whose whole culture and social organization is of Tibet. They have a well-developed system of farming on permanent fields. Their maize is grown as a pure crop in rotation with other cereals and in the permanent fields. It is sown in May and June, and is harvested from late September to early November. The lateness of the sowing as compared with other areas is due to the need of fitting it in with their system of rotation. Sowing is entirely by broadcasting, and the ears are pulled off by hand. The variety *Phentang* is the most grown, and is in large fields. The variety *Num Phentang* is grown in small amounts, and is relegated to odd corners, edges of fields and to the few areas of shifting cultivation. The introduced dentate maize, *Khana Phentang*, is almost entirely relegated to the areas of shifting cultivation. The reason for the different technique will be clarified below.

Uses: The Monbas, with their advanced economy, grow a variety of grain crops, all of some importance. These include maize, barley, rice, buckwheat, millets, *Chenopodium*, cockscomb. However, with the exception of a few villages at 9,000 feet and above, the most important crop is maize, which is said to be more important than the others put together, and is the staple food. The main uses of the grain are:

1. For the ordinary food, the variety *Phentang* is ground to a coarse flour by

means of the ordinary Tibetan water mill. The flour is usually boiled. This flour is known as *Phentang bukpu.*

2. A small proportion of the same variety is eaten when the ears are still soft.

3. The *Phentang* is slightly roasted and then flattened and partially broken up by light pounding. In this form it is chewed as a relish, especially while liquor is being drunk, and plates of it are always offered to visitors. The local name is *kakung*. A great deal is consumed in this way, and the *kakung* is also an article of trade in Tibet.

4. The *Phentang* is used to a fair extent in brewing of beer and distillation of a weak spirit. This is said to be the use of the introduced variety *Khana Phentang*.

5. For popcorn, the variety *Num Phentang* only is used, and it is grown for that purpose only. It is popped by heating in an earthenware vessel with a little sand.

As far as I know, virtually all the maize crop is used for human consumption only, except that the "leavings" from manufacture of liquor go to the pigs. By far the most important type is thus the *Phentang*, a strong-growing, large-grained golden-yellow or occasionally red, flint type.

Methods of Storage: This aspect is also interesting. When the maize is ripe, the ears are left for some weeks on the plant to dry. They are then gathered, and the enclosing leaves removed. The ears are then stacked on the fields in solid rectangular panels up to 20 feet long, by 10 feet high, and perhaps 2 feet thick, the structure being raised off the ground by a slight framework of sticks. The panels are often L-shaped. A field, when the crop is stacked, is a beautiful sight dotted with these solid patches of golden yellow, the more so since the few scarlet ears are suspended over the top for color effect[1]. The crop is left thus for a month or less to dry off thoroughly, after which the ears are carried home to the village, and the grain removed either by hand or threshing with a short stick. It is stored in large round baskets in the upper room of the two-storied house. The seed for next season is left on the ear and hung up on the rafters.

Traditions, folklore, etc.: The Monbas simply state that they have always grown maize, and that as far as their traditions go back it has been the staple food crop. On the other hand, they have a well-established tradition that they first got their rice from the Plains of Assam. By religion they are Buddhists (every other tribe in the Assam Hills is Animist), and it is both interesting and significant that the first ears of maize to be gathered are placed in the village temple as an offering, while they deny any such practice in the case of their barley which (together with their Buddhism) they must have obtained from Tibet. It is also a common sight to see a few ears of maize hung up as offerings inside the temple, or placed on small wayside shrines. I have asked members of the tribe if they have any special rites, dances or festivals for their maize, and in all instances this was denied. I would

[1] It is possible that the original purpose of suspending the red ears was to ward off evil spirits from the fields.

not, however, like to state categorically that my informants were accurate. In dealings with tribal peoples knowledge of religious custom can only be got by long and close acquaintance or direct observation.

21. THE APA TANI TRIBE:—

Varieties grown: Serial Nos. 1–4 of first consignment (as for Dafla Tribe).

Ecology and technique: The Apa Tanis, although a primitive people without writing, etc., have a very highly developed system of irrigated rice cultivation for their staple food supply, and practice shifting cultivation extremely little, if at all. The maize is grown in small quantities in little garden plots in and around the village. The tribe inhabits a small area in the Dafla Hills and the varieties grown are the same.

Uses: Maize is not an important crop. A proportion of it is eaten soft on the ear. Some is stored, and is prepared by first roasting it in a clay pot and then pounding it to a coarse flour. It is said to be eaten mainly by old people with decayed teeth, but this needs checking. Popcorn is prepared in considerable amounts, and is made by putting the grain into the glowing embers of the fire, and picking it out with bamboo tongs as it bursts. I am not sure if the other method of heating the grain in an earthenware pot is used.

Methods of Storage: The small quantity stored is kept with the rice in separate granaries.

Traditions, folklore, etc.: I have no information.

22. THE MISHMI TRIBE:—

I have once visited a small section of this very primitive tribe, and have only the scantiest information. Their shifting cultivation is rough and ready. Maize is included among the crops and Mishmis have told me that it is of moderate importance. I have seen Mishmi women making popcorn by putting the grain in the edge of the house fire, and picking it out as it bursts.

MAIZE IN HILL AREAS OUTSIDE THE BOUNDARY OF ASSAM

BHUTAN:—

I have talked to many traders and others from Bhutan and am told by them that maize is grown everywhere, and is a fairly important crop. A large yellow type is said to be the most widely grown, and is presumably the same as the *Phentang* of the Monba tribe on the Assam-Bhutan border.

SIKKIM:—

As for Bhutan. Writing a hundred years ago, Sir Joseph Hooker ("Himalayan Journals," Vol. II, p. 78, footnote) states that he was given popcorn in North Sikkim. He describes it as, "Called pop-corn in America, and prepared by roasting the maize in an iron vessel, when it splits and turns partly inside out, exposing a snow-white spongy mass of farina. It looks very handsome, and would make a beautiful dish for dessert." Hooker also records (Volume I, p. 157) seeing, in May, 1848, the maize just sprouting in North Sikkim. He goes on to record the

curious statement that "This plant is occasionally hermaphrodite in Sikkim, the flowers forming a large drooping panicle and ripening small grains: it is, however, a rare occurrence, and the specimens are highly valued by the people." Unfortunately, he does not tell us if he actually saw such plants, or if he was recording from hearsay.

Maize is among the crops of the small Lepcha tribe of Sikkim. In his book "Himalayan Village" (published in 1938) Mr. G. Gorer refers several times to maize cultivation. He notes (p. 95) that wheat and maize are used for food when rice is short, but states that "they are not liked." He notes that the maize is sown in March (p. 94). This is confirmed by Major J. Morris in his book "Living with the Lepchas" (1938, Chapter 9) where he several times refers to maize as being among the crops raised by this tribe.

NEPAL:—

Of this region, I have the scantiest information. Nepalese immigrants into Assam have told me that they grow considerable quantities of maize in their own country. Maize is an invariable crop of these immigrants, even when they settle in the hot plains of the Brahamaputra Valley. They grow large yellow or white forms, the same or very similar to the main type of the tribes of the Assam Himalayas (Abors, Daflas, Monbas).

BURMA:—

Unfortunately, I have been able to get no information concerning the Shans, Wa's, Karens, or any of the hill peoples in Burma except the Chins as recorded above. Of the large Kachin tribe, who live in the extreme north of the country and whose hills are contiguous to the Mishmi Hills of Assam, Mr. J. L. Leyden has recorded (introduction to a pamphlet "The Kachins of the Hukawng Valley" by Kawlu Ma Mawng, 1944, p. ix):

> The Kachins are rice eaters, and their agriculture is mainly concerned with the production of their staple food. Kachin agriculture is chiefly concerned in the extremely wasteful and inefficient shifting cultivation . . . . . As the cultivation and sowing is crudely carried out the Kachins invariably find themselves with a poor crop of rice and are compelled to work subsidiary crops of maize, millet and yams to avoid starvation.

While this somewhat bald statement as to why maize and millet are grown can hardly be accepted at its face value, especially *vis a vis* the tribes of Assam, it at least indicates that maize is an established subsidiary crop, probably in very much the same way as among the Naga tribes.

MANIPUR STATE:—

The Naga and Kuki tribes of Manipur State are of the same stock as those of the southern Naga Hills (see above under Cachar Nagas and Kukis), and it is reasonably certain that they grow the same maize and in the same way as do their neighbors. The Manipuris proper inhabit the highly irrigated plain of the Manipur Valley. I have no information as to whether they grow maize, but consider it unlikely that it is of any importance as their fields give them a considerable surplus of rice.

HISTORY IN THE ASSAM HILLS

As we have seen, maize is grown by all the multifarious peoples of the region. This wide distribution does not in itself mean that it is of necessity an ancient crop. Once introduced and given favorable conditions for its spread, any crop can spread with rapidity, even in remote areas during a very few generations. This has taken place in the Assam Hills, a good instance being the potato. Another such crop is manioc, which is now grown in at least three widely separated ranges of hills. But both these crops are universally recognized as being introduced after the coming of the British. In the Garo Hills I was told by illiterate villagers that manioc has been grown by them for about twenty-five years; and in the northern Naga Hills it is said to have been with them for two or three generations. But in the case of maize I was simply told by every tribe that they have always had it among their crops, and any suggestion that it came from outside was ridiculed. An exception to this, as recorded above, is the Aka tribe, a small tribe of the Assam Himalayas, who believe their maize to have been obtained from neighboring tribes many generations back. I have constantly inquired in tribal villages, and particularly among the old men of the community, as to when and how they first got their main crops. The reply was always the same in regard to millets, taro, maize, Job's-tears, and yams. They have always been grown, and no one can say when or how they were first obtained. In some cases this is true with rice, now the staple crop among the majority, but there are indications that rice is a more recent food than the rest, although it is undoubtedly a very ancient crop and has been grown in Asia for some thousands of years. Thus, among the Chang, Yimchungrr, and some of the Konyak Nagas, the people even now depend on roots and cereals other than rice for their food supply and state quite openly that they are older crops, maize not excluded. The same is true of the Monbas, who have a definite tradition that maize has "always" been their main crop, while rice was obtained many generations ago from the Plains of Assam.

Furthermore, in the case of rice there are established legends to account for its origin. They have been recorded for the Naga Tribes by Professor Hutton and Mr. Mills (in the series of monographs on the Naga Tribes), and for the Lakhers by Mr. Parry ("The Lakhers," 1928), while I myself have been told folk tales by the Daflas, Minyong, Abors, and Khasis. But there is no legend known to account for the origin of the other cereals, millet, maize, and Job's-tears, the inference being that rice is more recent while the others are lost in the mists of antiquity.

The existence of a distinct name for maize is everywhere indicative of a respectable age, the more so when we note that in several cases where a variety has been introduced by the British or by Nepali immigrants, the fact is well-known. Among a few tribes, notably the Khasis and the Lhota Nagas, the tribal name is indicative of origin from neighboring peoples. This is not, however, quite conclusive, as the generalized name could be based on a variety got from the tribe in question and which supplanted older and more indigenous types.

My notes on the religious aspect are particularly scanty. However, the dance of the Lakhers, the use of maize in funeral rites among the Lushais in deliberate preference to rice, its importance as a votive offering among the Monbas, the part it plays among the agricultural ritual of the Rengma Nagas, and the existence of a special tutelary deity among the Chang Nagas, all point to its being a well-established crop, the more so since primitive peoples with animistic religion are invariably shy of incorporating new crops into their agricultural ritual.

The wide distribution, the positive statements of the peoples themselves, the position relative to the crop complex, the existence of distinctive tribal names, and the place in religion, all point to a long history, going back for centuries at least, for maize among the hill tribes of this region. As we shall consider immediately, this is fully supported by the general economics of the crop and the variety of uses to which it is put.

GENERAL ECONOMICS

This is a major study in itself, and the factors involved are many. Among them may be listed: (1) climate; (2) the varieties available; (3) techniques of cultivation; (4) other crops grown; (5) uses for which the crop is grown.

Taking first the climatic factors, the *climate* of the Assam Hill areas varies from sub-tropical to sub-temperate, and maize is grown at all elevations from a few hundred feet to 6,000 feet. In general, it is of more importance to the tribes living at high altitudes, a state of affairs not unconnected with absence of rice varieties suitable for cold elevations, as among the Chang Nagas and surrounding tribes, and possibly among the eastern branch of the Lushais and the Chins.

Varieties grown in any one area or by any one tribe are clearly dependent, within the limits of the climate, on the culture contacts, the purpose for which maize is needed, and so on. There is a far greater variety of types grown along the Assam-Burma border (Nagas, Lushais, and Chins) than in the outer Himalayas (Abors, Daflas, Monbas), although maize is on the whole more important in the Himalayan region. Since all tribes of the Himalayas store part of their maize, inspection of granaries after the crops had been harvested have enabled me to survey with reasonable accuracy the varieties grown, and the peoples of this region seem to cultivate only the larger coarser types, the small several-eared forms being entirely absent and apparently confined to the Assam-Burma border. These very distinctive small varieties are moreover grown at low altitudes, and I do not think them to be cultivated at elevations higher than 4,000 feet, so that they are all associated with the sub-tropical rather than the sub-temperate zones.

Although the climatic conditions of the inhabited parts of the Himalayas are, on the whole, colder than in the other hill areas with which we are concerned, there are thickly populated areas in the low sub-tropical foothills of the Abor country which are very similar to the outer Naga Hills; and the inference is that the tribes of the Himalayan region have never had these small maizes. This seems to link up

with the larger number of tribal groups in the Burma region and the greater frequency of migration to and from the area, as well as local movements within these particular hills, each group contributing its quota to the complex of crops over the passage of time and passing them on by local diffusion. Leaving aside any possibility of a variety having originated at some remote period in the area where it is now grown, each tribe seems to have accumulated its types of maize by culture contact.

For reasons given I do not consider that there has been any great production of varieties by hybridization. In the data recorded above some support is given to this origin of varieties within a tribe. Thus the Lushais regard a proportion of their maize varieties as their own, one as obtained from their Chin neighbors, and two as of recent introduction from the Nepalese and the British. The Lhota Nagas of the hotter foothills have three varieties they regard as indigenous, or at least of very ancient introduction, one obtained from the Angami Nagas, one from the Ao Nagas, and one from the Nepalese. It is stressed that the word "indigenous" implies only that a variety has been grown for a period for its ultimate origin to have been forgotten in the traditional memory of the tribe, and in no case necessarily means that it originated with them.

Technique of cultivation:—As indicated already, in the majority of cases the maize is grown in lines, small patches, or single plants among the other cereal crops. Only among the Monbas with their advanced farming, the Angami Nagas and the Apa Tanis with their system of irrigated rice growing, and perhaps among the Lushais, the Chins, and Akas, is it normally a pure crop. At first sight, this rather haphazard technique seems conducive to hybridization, particularly where five or six types are grown by a single village. But examination of granaries shows but a small proportion of parti-colored ears. The reasons are not far to seek. In the first place, there is a general prejudice which I have often heard expressed against saving seed from any plants which do not look pure bred; secondly, as I have demonstrated by experiment, different types flower at long enough intervals apart to act as a fairly effective check on cross-pollination; thirdly, all types are not extensive, but in every area I have visited, a walk through the fields shows different types grown in different stretches of land and certain types are definitely looked on as more suited to distinct soils and elevations . In clarification of this, it is important to remember that a village community cultivating on hill slopes will almost invariably have in use at any one time fields varying up to several hundred feet in height above sea-level, with corresponding diversity of exposure to winds, etc. It therefore stands to reason that where different varieties of any crop are grown they will be dispersed according to individual suitability to local variations in climate and soil conditions. As a general rule I have seen the larger-grained types of maize relegated to the higher-altitude fields, while the small popcorns and several-eared forms are sown on the lower, warmer slopes. Finally, the tribes are perfectly well aware that sowing different varieties mixed together leads to the

hybridization they are anxious to avoid, and for obvious reasons deliberate segregation is practiced.

Uses to which maize is put: Within the limits of the climate and the varieties available, the purpose for which maize is grown is naturally the determining influence of every aspect of a crop, maize as much as any other. As the whole background of the economics, is the major fact that in the Assam Hills *rice* is the cereal crop preferred above all others, and wherever it can be grown and suitable types are available it is now the staple cereal. In qualification of this, we have already referred to maize as being the main grain crop among the Monba tribe of the Assam-Bhutan border. Members of the tribe have, however, told me that they prefer rice when they can get it, but since their arable land is limited and there is very little fit for irrigation, it is more economical to grow maize as a main crop. In a somewhat similar way, among the Chang Nagas and neighboring smaller Naga tribes, millets, maize, and Job's Tears are the most important cereal crops largely because the people have no rice varieties suitable for the cold altitude of their lands. Within the past two or three years the Chang tribe has made requests to the government to help obtain seeds of rice suitable for this cold climate. I do not know if this applies among the eastern Lushais and the Chins, but the inference is that it does, since the Lushais dwelling in warmer parts of the hills are all rice cultivators. The detailed uses of maize as outlined above are:

1. A catch-crop, eaten while the grain is soft. (All tribes.)
2. Stored for food in the winter, either as a reserve secondary to rice, or more occasionally as a main crop.
3. For beer-making.
4. For popcorn.
5. For pig food.
6. As an article of trade outside the village.

The first named is the most universal use of the crop, and applies to all tribes. For eating fresh, as a catch-crop, the smaller, several-eared types (other than the popcorn) are often preferred by those who grow them. This is apparently due to their soft, sugary grains which are appreciated both in themselves and as an alternative to the harder less sweet types. I think this to be the main reason for survival of these small types, since the grain is not nearly so economical for storing as winter-food as are the larger, "coarser" forms, and I know of no tribe which stores the smaller varieties for any purpose other than popcorn and perhaps for beer *(vide infra)* to a very limited extent. A point of some importance in connection with the use of maize as a catch-crop and for immediate consumption is the fact that different types grown in the area in question differ very appreciably in the time taken to mature, the small several-eared forms being several weeks slower than the larger types. It is of course well known to the peoples who grow them, and who naturally therefore space out the crop on this basis, to cover as long a period as is necessary.

The dried, ripened grain stored for the winter is, as we have seen, of primary importance among the Monbas, Changs and neighboring tribes, the Chins, and Eastern Lushais. It is of secondary importance among the Daflas and the Abor tribes, and the Sema Nagas, and is of fairly minor importance among the rest. It is, however, essential to maintain a balanced perspective and to remember that while statements of this kind are accurate in general terms, the whole balance of crops and their use is naturally fluid, especially among a primitive tribe with a comparatively unstable economy, and any general picture is only true for the actual time a survey is made. Thus, local conquests of tribe by tribe were taking place in the Naga Hills and elsewhere before British Administration was introduced, conquests which were accompanied by varying degrees of change in the pattern of culture, the crops not excluded. Nor has change ceased since more settled administration was started. In most hill areas of Assam, the government has constantly been trying to persuade tribal peoples to change over from shifting technique for mixed crops to permanent irrigated cultivation for rice.

Similarly, in a more restricted sense still, a season of poor rice harvest in the autumn means that the supplies for the winter and following spring will soon be exhausted, and under these conditions a people such as the Daflas who normally consume a proportion of their maize as it ripens and store a proportion for beer and a reserve of food during the winter, will naturally use a greater amount for food and less for liquor, and *vice-versa,* after a good harvest, when there will probably be even a little to spare for the pigs. To narrow this down even further, from the tribe or the village to the individual household among peoples for whom rice is the most important of many crops, the subsidiary crops of maize, millets, and roots are naturally most important for the poorer people of the community whose rice supply runs out before the end of the season and the start of the next year's main harvest, and who live rather from "hand to mouth" depending to a greater or lesser extent on the "catch-crops" for their main food supply.

The use of maize for beer is governed by the same factors as for food. Among most tribes rice is preferred for beer-making. Possible exceptions to this are the Sema Nagas, who seem to use maize from choice, and the Eastern Daflas, who grow considerable quantities of millet solely for beer. It follows as a natural sequence that the worse the food crops in any one season, the less will be spared for beer and the more will be needed for human consumption. Very often beer is made from a blend of a variety of ingredients, the technique varying even from village to village within the same tribe, and maize will normally be included in the list of grains used for the brew. Thus, among the Chang Nagas I have been told that beer is made by mixing maize, Job's-tears, millets, and *Chenopodium* in fairly definite proportions. I have not been able to discover that any maize variety is used or grown specifically for beer, but this is a point calling for more detailed investigation.

Popcorn is used everywhere, and special varieties are normally grown for this purpose only. The popcorn is made either by roasting the grain in a pot, often mixed with a little sand, or by simply placing the grains at the edge of the fire and picking out the popped grains with bamboo tongs as they burst.

The above notes deal with maize among the tribal peoples of the Assam Hills, and the plains areas of the Brahamaputra Valley and the southeast of Assam and Pakistan have not been considered since maize is not grown there by the indigenous population. It is, however, possible to grow it in the plains, and it is a common crop among Nepali immigrants. It is therefore perfectly feasible that it was grown in past epochs by the aboriginal population of the Assam Plains who might well have abandoned it with the development of a highly organized system of irrigated cultivation for rice.

Part II

EDGAR ANDERSON

The data reported in this paper are basically simple, being essentially a morphological survey of the varieties of maize grown by the Naga. However, the accurate assembling of these critical data required the cooperation of a number of individuals and institutions. The varieties collected by Stonor were numbered by him, and selections from most of them were grown in his experimental plot in Shillong, Assam. Herbarium specimens of the tassels and photographs of several of the more outstanding varieties were then forwarded to the Missouri Botanical Garden. Samples of the original ears collected by Stonor were sent to the Royal Botanic Garden at Kew where they were photographed. The ears were then shelled and the seeds, identified by their original numbers, were sent to the United States, where they were fumigated and forwarded to the Missouri Botanical Garden. The empty cobs were imported separately and were sterilized by heat before being released. These extraordinary precautions were necessary because two of the worst diseases of maize are found in southeastern Asia. At the Missouri Botanical Garden samples of the seeds were germinated and the seedling characters were studied. Several representative cobs were turned over to Dr. L. W. Lenz for histological examination and were included in his recent (1948) survey. Early the following spring the seeds were forwarded to Dr. E. G. Anderson of the California Institute of Technology where they were planted in the maize-breeding plot at Arcadia, California, one of the most favorable sites in this country for tropical maize. With the cooperation of Dr. A. E. Longley of the U. S. Department of Agriculture and Dr. William L. Brown of the Pioneer Hi-Bred Corn Company, material for cytological examination was obtained from many of the cultures and chromosome knob numbers and knob positions were determined from pachytene smears. During the growing season I worked at Arcadia for ten weeks where all the cultures, aside from a few late-maturing varieties, were scored for plant color, representative plants

were photographed to scale, herbarium specimens were made of tassels, internode diagrams were made of mature plants, and the details of tassel and ear morphology were recorded. Eventually all the data and materials were assembled at the Missouri Botanical Garden—the herbarium specimens and photographs from Shillong, the photographs and shelled cobs from Kew, the photographs, herbarium specimens, and notes from California, the knob counts made by Dr. Brown and myself, and the histological information from Dr. Lenz. We are also indebted to Dr. Herschel Roman and Mr. Earl Patterson for internode measurements and specimens of varieties which matured after I left California.

The following collections were grown; the information concerning each variety was supplied by Mr. Stonor:

Serial No.	Locality	Tribe	Remarks
1	E. Dafla Outer Himalaya	E. Dafla	Sown Feb.–March; ripe June. Much grown at 3000 ft. Local name *Topothe*. Number of ears 2–4.
5	N. Cachar Hills	Kuki	Grown at 2000–3000 ft. Number of ears 4–5.
6	N. Cachar Hills	Kuki	As for 5, with which it is grown.
7	N. Cachar Hills	Zemi Naga	Grown at 1500–4000 ft. No precise details. Said to give 2–3 ears. Sown about March.
8	N. Cachar Hills	Zemi Naga	Grown at 2000–3000 ft. Said to be slow-ripening. Gives 4–6 ears. Sown about March.
9	Naga Hills	Angami Naga	Grown at 3000 ft. Details as for 8.
10	Naga Hills	Angami Naga	Grown at 3000–4000 ft. No other details.
11	Naga Hills	Angami Naga	Grown at 3000–4500 ft. No other details.
12	Naga Hills	Ao Naga	Grown at 3000–4000 ft. Sown Feb. to March; ripe June–Sept. Said to bear 7–8 ears. Local name *Lozar*.
13	Naga Hills	Ao Naga	Grown at 3000–4000 ft. Sown late March; ripe June–July. Has 3 ears. Said to be very sweet. Local name: *Mapok Memdi*.
14	Naga Hills	Sema Nega	Grown at 3000 ft. Sown March to April; ripe June to July. Has 3–4 ears. Local name: *Azheu*.
15	Naga Hills	Sema Nega	Grown at 2000–3000 ft. Sown March–April; ripe June–July. Said to have 6 ears. Local name *Azehuge*.
16	Naga Hills	Sema Nega	Grown at 2000–3000 ft. Sown March; harvested July. Said to be sweet. Has 2–3 ears. Local name *Meshcu*.
17	Naga Hills	Sema Nega	Grown at 3000 ft. Sown March–April; ripe June–July. Has 2–3 ears. Local name *Kolami*.
18	Naga Hills	Sema Nega	Grown at 2000–3000 ft. Sown Feb.–May; ripe May to Sept. Has 6–7 ears (verbal report). Local name *Anila*.

In addition, seven varieties collected in the Lushai Hills were grown. Since they were in general very similar to the above and included no peculiarities not represented in the Naga collection, no detailed account of them has been prepared.

General Appearance:—

As compared with most collections of native varieties from South and Central America, one of the most outstanding characteristics of these Assamese varieties was the uniformity of several of the varieties and their differences from each other. This bears out Mr. Stonor's remarks as to the skill and determination of the Naga in keeping their varieties pure. Several of the cultures, though grown directly from seeds collected among the Naga, were as uniform as a good inbred line. It is probably significant that those varieties which were most unlike anything previously known in our studies of exotic maize were the most uniform, while the one variety most closely resembling the maize of Latin America was among the most variable (see below under "Caribbean"). The conspicuous differences between certain of the varieties make it difficult to generalize about them as a group; nevertheless there were certain definite trends which characterized the entire collection. Almost without exception these trends were most strongly marked in those kinds which morphologically were the most extreme such as "Late Upright" and "Late Sidewise."

Fig. 1. Internode diagram of one plant of Stonor 18 ("Late Sidewise"), grown at Arcadia, Cal. Circles represent tassels, elliptical figures ears. The diagram is as if the stalk were cut at the nodes and the dissected internodes were laid side by side in succession, the lowest at the left, the uppermost at the right, and then a line (the line seen in the diagram) were drawn connecting their summits. The scale at the left (in centimeters) indicates the lengths of the internodes. It will be noted that there were over 30 nodes on the plant, none of which was over 8 cm. long; that there 4 ears; and only 4 short internodes between the upper ear and the tassel. Small lines at the left of the diagram indicate nodes at which there were well-developed prop-roots.

Figure 1 shows a drawing to scale of a typical seedling. The short, narrow tap-root, the numerous adventitious roots from the mesocotyl, and the broad mesocotyl and coleoptile are characteristic.

One of the most unexpected characteristics of these varieties was their green color. Not only were they mostly without the bright plant, tassel, and silk colors of so many Latin American varieties, but some of them had no visible anthocyanin pigment in any part of the plant. The group as a whole had a strong tendency to green silks, green anthers, green leaves, and green culms. There was also a strong tendency for the leaves to have a more evenly green appearance, like certain varie-

ties of *Sorghum*. In nearly all the maize of the New World there are minute differences in the intensity of the green above and between the veins, giving the leaves macroscopically a kind of longitudinal grain. The Assamese varieties tended to be evenly green throughout like a green plastic dish.

The collections among the Naga were outstanding in their lack of vigor, and this was quite as true in Shillong, Assam, as in Arcadia, California. Some were mid-season, others late or very late, but all of them developed slowly. From the time the tassel made its first appearance until it was completely out of the leaves and shedding pollen, as much as four weeks might elapse. One of the most outstanding characteristics of the maize of the New World is its vigor. Nearly all maize varieties grow and develop rapidly; the controlled heterosis of hybrid maize is merely an extreme standardized example of a tendency nearly universal in the New World. This vigor was absent in the Assamese varieties. Whether midseason or late in their maturity they poked along from week to week. The internodes were short; in the most extreme variety none of them was over 10 cm. in most plants. Nor was this the result of their having been transplanted from Assam to California, since the samples grown by Stonor in Shillong exhibited these same characteristics.

The internode patterns were highly peculiar. In addition to short internodes, the varieties from the Naga tended to have many ears (as many as four or five in some varieties), and the internodes above the ears were so short and crowded that the silks of the uppermost ear were sometimes tangled in among the lower branches of the tassel (see plate 22). Not only were the upper leaves crowded together but as Collins noted (1909) in his description of waxy maize from the Orient, they all tended to be gathered at one side of the culm and to hang over the developing tassel like a kind of spathe. While this character was more extreme in some varieties than in others, there was a marked tendency in that direction throughout the collection.

The arched and drooping spathe-like upper leaves were accented by the drooping and semi-included tassels. Tassel branches tended to be more slender than those of New World varieties, and in the more extreme varieties they hung down vertically until after the pollen was shed or even later. Though the tassel branches were long, the glumes were small. Because of the short upper internodes the tassels were never exserted from the upper leaves as pollen started to shed and many of them were not exserted even when fully mature.

For the ear the prevailing tendencies of the collection were to small cobs, prominent glumes, small, isodiametric kernels, and complete absence of row-pairing. The colors of their kernels were mostly a pale straw-yellow or a dull reddish-blue.

In their even green color, included tassels, slender culms, slender tassel branches, isodiametric kernels, straw-colored or dull blue kernels, these Assamese varieties resembled sorghum more closely than do New World varieties of maize, and one

variety even had a bluish-green bloom on its leaves rather similar to that which is so characteristic of certain varieties of sorghum.

Among the collections from the Naga a number of different sub-types could be distinguished. It seems unwise to dignify them with permanent names until we know more about the kinds of Oriental maize than we do at present. For the purposes of this discussion they may be provisionally designated as follows: I—Caribbean; II—Early Slender; III—Late Upright; IV—Early Upright; V—Late Sidewise; VI—Drooping Waxy. Some of their characteristics are shown in tabular form in table 1.

I—*Caribbean:* Types of maize fairly similar to those grown around the Caribbean basin are widely distributed in the Orient and were apparently introduced by the Spanish. They seem to be the prevailing type in the Philippines and in Guam and they or mixtures with them make up the bulk of the maize grown in Asia, particularly at lower elevations and along the coasts. In previous years I have grown collections from India, Guam, the Philippines, Sumatra, the valley of the Irrawady in Burma, and from China. One such variety was collected by Stonor (No. 17), though he commented as follows: "Evidently not quite a pure strain." The ear-to-row test of this collection showed more plant-to-plant variation than did Stonor's other collections among the Naga. In it the distinctive characters of the rest of the collection are less strongly developed. It grew more quickly, had more pronounced plant color and colored silks, it had coarse tassels, large ears with white kernels conspicuously capped with soft starch, and was the earliest of anything in the collection. It showed Assamese tendencies in its somewhat included tassel. It probably represents a fairly recent mixture between Assamese maize and one of those Caribbean types which were spread so widely around the world by the Spanish and the Portugese.

II—*Early Slender:* In its slender stem, long slender leaves, and most pronounced spathe at flowering time, this variety was very similar to VI. It differed in being the earliest of the distinctive varieties and in the morphology of the mature tassel. Although the tassel branches were completely pendent when they first appeared and even after they began to shed pollen they eventually stiffened to produce a tassel more like broom-corn than any other known variety of maize. The long, slender, wiry branches became stiffly distended when mature, and the small glumes (5–6 mm. long) were quite closely appressed. As in many of the varieties with short upper internodes, the auricle of the uppermost leaf was developed into a conspicuous tuft of long white hairs. Though to casual observation this variety seemed to be completely green, careful examination at the base of the plant showed a faint flush of color.

III—*Late Upright:* The leaves of this type were dark green, were held crisply erect until after the tassel appeared, and were twisted, usually one complete revolution and sometimes more. The plants had many short internodes and grew and

TABLE I

CHARACTERISTICS OF NAGA VARIETIES

Type	Stonor No.	C.I.T. No. 1948	Row Number	Kernel size in mm.	Kernel shape	Midcob width in mm.	Pith diam. in mm.	Base color	Tassell inclusion	Pendent tassel	Season	Chromosome knob number	Kernel color	Number of ears
I—Caribbean	17	1088	14	Large	Flat	26	11	+	Faint	Slight	Early		White	1
II—Early Slender	13	1084	14	Medium	Square	20	6	—	Strong	Medium	Early		Lt. yellow	1
III—Late Upright	5	1076	14	Small	Sphere	20	7	0	Strong	Strong	Early		Dull blue	4
	8	1079	20	Small	Sphere	22	11	0	Faint	Strong	Very late		Purplish	3
	9	1080	20	Small	Sphere	22	8				Very late	4	Dull blue	
	10	1081	16	Small	Sphere	19	7	0	Faint		Late	5–7	Dull blue	
	14	1085	14	Large	Subsphere	18	12	+			Late		Red-purple	
IV—Early Upright	6	1077	10	Very small	Sphere	18	3	+	Strong	Medium	Early		Red	4
V—Late Sidewise	11	1082	16	Small	Sphere	23	7	—	Strong		Very late	4–6	Lt. yellow	3
	12	1083	12	Small	Sphere	18	4	+	Strong		Very late	2	Or. yellow	4
	18	1089	14	Small	Sphere	19	4	+	Strong		Very late	4–5	Lt. yellow	4
VI—Drooping Waxy	16	1087	16	Small	Sphere	30	7	+	Strong	Strong	Mid-season		Ivory	2

developed slowly. The internode pattern of a typical plant is shown in fig. 1. The kernels are small, with a dull, purplish blue aleurone and are used as a popcorn (see Stonor's notes). Similar popcorns (as well as the actual popped kernels) have been received from correspondents in Siam. Stonor's different collections made among various Naga tribes were almost identical in growth type aside from one or two obviously out-crossed individuals. In their small kernels, upright twisted leaves, large number of ears, and pedicel and cob anatomy, this type resembles certain ancient popcorns of South America. Ears and popped kernels have been obtained from various graves and trash-heaps in coastal Peru and Chile (Anderson, 1947), and through the kindness of Dr. Paul Weatherwax a living example of such a popcorn was grown from one of Parodi's collections in Argentina. Since Ica times (the Ica preceded the more widely known Inca) these kinds of small-kernelled popcorns have been rare. At earlier times they were apparently the prevailing type along the coast of Peru and Chile and have been recovered from graves in the Argentine. A somewhat similar popcorn, of unknown origin, is sometimes grown in the United States in spite of its long season and small ears, because of its high quality. Though it has been extensively confused with the early-seasoned "Tom Thumb," its proper name is apparently "Ladyfinger," by which name it was first called in the United States at least a century ago (Emmons, 1849).

The tassels of Late Upright plants exhibited little or no condensation and from slight to pronounced multiplication (Cutler, 1946). The central spikes were prevailingly in whorls of three. Most of the plants grew four good ears with partly developed nubbins at lower nodes. Collection Nos. 5, 8, and 10 showed no base color (in other words they were like '*aa*' plants) and No. 14 which showed base color had larger and redder kernels and may well have been derived from a cross between a typical Late Upright and some other sort of maize. One cob of No. 8 was examined by Lenz (1948) and is figured by him, plate 38, fig. 5. It has the longest, slenderest pedicel ever reported for any variety of maize.

IV—*Early Upright:* This one collection (No. 6) was in every way like the Late Uprights except that it was earlier, had red seeds, and pronounced base color.

V—*Late Sidewise:* Both in Assam and in the United States this variety in the vegetative stage looks unlike anything previously reported for *Zea Mays*. The leaves and especially the culms are bluish-green with a distinct bloom. The tillers are practically horizontal during the first month or so of their development. On both tillers and main culm the internodes are very short, and even in the mature plants few ever exceed 10 cm. in length. Most agronomists, seeing the plants before they had tasseled out, would have wondered if they were some kind of sorghum. Base color varied from very faint to strong, and the leaves, even early in development, stood out at right angles to the culm. The ears were long and slender with small yellowish kernels. The large number of internodes (30 or more

per plant) was evidently not a response to a longer day length, since similar results were obtained in Shillong and since there were prop-roots at only one or two of the lower nodes. (In tropical maize grown in the United States there may be prop-roots on 10 or more nodes as one result of the change in length of day.)

VI—*Drooping Waxy:* Up to flowering time this variety was much like II except for the later season and consequent higher number of leaves. It had the same slender culm, slender green leaves, and, if possible, an even more highly developed spathe from within which the slender tassel branches drooped straight downward. Even at the end of the season, both in California and Assam, the tassel, though arching horizontally, was still quite pendent and much more extreme than any tendency of this sort in South American maize. All the plants of this variety had waxy pollen, and an analysis of the kernels at the Northern Regional Laboratory at Peoria, Ill., bore out this diagnosis. Stonor reported the young ears as being outstandingly sweet, and, like much of the waxy maize in the Orient, this is probably a specialized type used for green corn. Waxy maize is cultivated in the vicinity of Chungking, China, as a table corn, and Kuleshov's monograph (1928) illustrates the same pendent tassel in waxy varieties from various parts of Asia.

To summarize: These remote Asiatic aborigines cultivate a number of exceptionally well-differentiated varieties of maize. The following unusual characters typify one or more of these varieties:

Uniformly green leaves, culms, silks, and anthers.
Slender, pendent tassel branches.
Straw-yellow endosperm, dull bluish-red aleurone.
Small, isodiametrical kernels.
Many short internodes, lack of vegetative vigor.
Upright, twisted tassel branches, short silks.
Tassel included in upper leaves at flowering time; leaves immediately below it falsely monostichous, forming a sort of spathe; tassel not completely exserted even when mature.
Waxy pollen and endosperm.

As we shall demonstrate below, this complex of characteristics is widely distributed in the back corners of Asia. It would be of primary significance to know where it is most closely approached in the New World. Certainly nothing like it is known from Mexico, Guatemala, or other parts of Central America. The only United States variety showing any of these characteristics is "Ladyfinger" popcorn, a variety of unknown origin which has been in this country for at least a century (Emmons, 1849).

In South America this complex of characters is rare, and most of the collections and published descriptions demonstrate radically different types of maize throughout that continent. However, a popcorn collected at Chiu Chiu, a remote oasis in

the Atacama desert of northern Chile, by Carl and Jonathan Sauer, has a number of features in common with these Oriental varieties (Anderson, 1943). Furthermore, as mentioned above, an indigenous popcorn collected in Argentina by Parodi, shows many of these same characters. A photograph by Jonathan Sauer of still another variety from Chiu Chiu, Chile, shows the multiple ears, the short silks, and the short upper internodes of the oriental varieties. In a collection of native corns from the Bolivian edge of the eastern lowlands, kindly turned over to me by Dr. H. C. Cutler, there were several plants which had the green plant color, pendent tassels, multiple ears, and spathe-like upper leaves of the Oriental varieties. Dr. F. C. Brieger informs me that he noted some of these same characteristics in other collections from these valleys. Insofar as one can judge from characters of the mature ear, a fairly similar set of varieties was once common on the west coast of South America. All the collections of early prehistoric maize from that area (and the museum material is so rich that it has not yet been possible to measure and record all of them) shows a small-cobbed variety with isodiametrical kernels, much of it apparently a popcorn, since the prehistorically popped kernels are known from a number of sites. This type, uniform in the lower archaeological levels, became gradually more variable and was supplanted by larger-kernelled types similar to modern Andean maize, when the Icas extended their influence down to the coast in times preceding the Inca domination.

In the Orient, on the other hand, similar varieties are widely, though very spottily, distributed. They are associated with the most primitive cultures in southeastern Asia, principally with the Tibeto-Burmans and allied peoples. In 1909 G. N. Collins published an exhaustive account of a variety of maize with a waxy endosperm which had been collected in China. In 1920 the same author, in a short communication, reported that waxy maize and other curious varieties had been obtained from the hill tribes of Upper Burma. Collins' description of waxy maize would apply equally well to most of the Naga varieties:

> While in only about 25 per cent of the plants were the upper leaf blades completely monostichous, all of them showed a tendency in this direction. This one-ranked appearance is brought about by a twisting of the leaf sheaths, the actual insertion of the leaves being opposite as in all grasses. In addition to the unusual position of the leaves the blades of the upper nodes were erect instead of spreading or dropping as in other varieties . . . . The internodes on the upper part of the plant were also much shortened, so that the tassel was not carried up, as in other varieties (loc. cit., p. 8).

His description (loc. cit., p. 13) of the aleurone color is also applicable to many of the Naga collections:

> The color of the aleurone layer was distinct from anything that has been observed in other varieties. It varied greatly in intensity. In rare cases it approached the bluish black of our common "black" varieties, but for the most part varied from a dull ruby to maroon. The color was usually confined to the top of the seed, fading out toward the base.

Under Vavilov the Russians made a comprehensive survey of Oriental maize which was reported upon by Kuleshov in 1928. It is extensively illustrated and accompanied by a summary in English (pp. 371–374). It demonstrates that

varieties similar to those described from the Naga country are widespread in central Asia from Persia and Turkestan to Tibet and Siberia. Figure 6, a variety from Persia, shows the characteristic short silks described by Collins and fig. 11 (3–6) shows tassels covered by a spathe of leaves in Persian and Turkestan varieties. Extremely pendent tassels from a number of points are described and illustrated. On pages 373–374 Kuleshov summarizes his morphological evidence.

> Asiatic maize shows a series of characters which are either unknown or very rare in American[1] maize. These characters manifest themselves in connection with a definite area, sometimes a very large one. Thus the waxy endosperm is spread from 5 to 45° North lat.; the short plant habit is peculiar to the vast expanse of Central Asia; panicles covered by the upper leaves and silks hiding in the axil of the leaf are met with in specimens from eastern Asia to Transcaucasia, etc.

The question of the introduction of maize into the Orient was gone into exhaustively by B. Laufer (1909). He came unequivocally to the conclusion that it was not introduced into China from the coast like other American crops but spread overland via Tibet. He was an accomplished linguist and bibliographer but without botanical training and had had to take the word of the botanists of his day that maize in the Orient was morphologically not different from maize in the New World. With this as a premise he could have come only to the conclusion he finally reached: that maize somehow got to Indian ports at an early post-Columbian date and spread overland via various primitive peoples to China. He quotes no botanical authorities for the morphological equivalance of Asiatic and New World maize, merely stating (footnote p. 224) his premise "If maize were indigenous to Asia, we should expect to find there either a wild form, from which the cultivated species are derived, or the Asiatic species to be differentiated from that of America, neither of which is found." Had the botanists of his day studied Oriental maize in even a cursory fashion they would have found that Asiatic maize is indeed "differentiated from that of America," most particularly in that very area between China and India which Laufer decided must have been the route by which the crop eventually reached China. His monograph is a mine of information as to the frequency of maize among these various primitive peoples and the role it plays in their economy:

> In the remarkable culture of the small mountainous tribe of the Lepcha in Sikkim, a people closely related in language to the Tibetans, maize plays a significant role, and it is surprising to note what a rich terminology they have developed with regard to its economy. There are four words for maize, two for the flowers of maize; and no less than eighteen varieties, by means of attributes are distinguished. Further the head of maize has several names according to its growth. There is a special expression for the young head when first appearing, for the head when seed commences to appear, when the grain begins to get a little larger, when the grain begins to get a little firm, when the grain has acquired firmness and for the head when ripe! [loc. cit., p. 242] . . . . It is interesting to note that among all the so-called aboriginal tribes of western and southern China, maize forms the favorite and principal food and is more highly appreciated by these tribes than by the Chinese. [loc. cit., p. 244].

---

[1]It should be emphasized that Kuleshov (1930) produced a monograph on the collections of maize made by Vavilov and his collaborators in Central and South America and was probably as familiar with the morphology of New World maize, as a whole, as any other investigator.

Laufer quotes (loc. cit., p. 245) B. C. Henry who says that in China maize "is now very extensively cultivated by the Chinese, but especially by the aboriginal peoples, among whom it seems to be almost as great a favorite as among the American Indians. It forms a main portion of the sustenance of both the aborigines in the north-western corner of Kwantung and of those in Hainan."

Through the courtesy of Dr. Ian Khambanonda it was possible to import a sample of a popcorn from Siam. It has violet-blue kernels similar to those of the Assamese varieties received from Stonor. Dr. T. W. Whitaker kindly grew a few plants of it for me at the U. S. Dept. Agr. Vegetable Breeding Laboratory at La Jolla, California. In its long season, upright leaves, slender tassel branches, short internodes, and large number of ears it closely resembled the Assamese popcorns. Popped kernels were also forwarded from Siam but Dr. Khambanonda was unable to supply very much detailed information because maize in Siam is grown principally by the aboriginal hill-tribes, seldom by the Siamese.

To summarize: A number of distinctive maize varieties are grown in the remotest parts of southeastern Asia, particularly by the aborigines of various hill tribes. Without exception it is more common among these primitive folk than among their civilized neighbors. In China it is more common and more appreciated among the aboriginal tribes of western and southern China than by the Chinese (Laufer, loc. cit.). Dr. Khambanonda testifies to its almost exclusive cultivation in Siam by the aborigines. Interviews with Ko Ko Lay, now an exchange scholar from Burma, have produced similar testimony for Burma. Dr. Pierre Larroque, the former maize breeder for Indo-China, tells me that among the primitive Meo, ethnologically related to the Tibetans, it is very commonly grown and that on the Yunnan border it seems almost to run wild. Mr. Stonor, the author of the first section of this paper, having been transferred to New Guinea, informs me that although it is either unknown or very recent along the coast, it is found among the primitive peoples of the interior. Its importance among the Lepcha of Sikkim and the aboriginal Li of the Island of Hainan has already been alluded to.

That maize could in post-Columbian times have spread to each of these various hinterlands without entering into the economies of the more civilized people who would have handed it on almost passes belief. Had it spread only to the Naga, one would have wondered what special circumstances caused its adoption by a people so remote that one ethnographer describes them as having lived for thousands of years "in these hills, as on some happy island, almost untouched by the waves of civilization which from time to time have surged through the plains of Assam and the valleys of Upper Burma. Ancient cultures which were once spread over great parts of southeastern Asia and which in most countries had finally to give way before the higher Indian and Chinese civilizations have been preserved here in a comparatively untouched form, and allow us to observe with our own eyes, early types

of human culture" (von Fürer-Haimendorf, 1939). Furthermore, when we examine the maize of these people it is not the dominant world crop of Central and North America. It is relatively unproductive and with less vigor than other known types of maize. To believe that in post-Columbian times maize could have penetrated not only to the Naga but to the hill tribes of Upper Burma, and of Siam, to the Lolo in central Asia, to the aborigines of Hainan, to the hill peoples of Sikkim, and to the interior of New Guinea, in each case passing over the more civilized peoples along the coast is beyond credulity. To have these conservative people somehow learning to use maize as a popcorn and as a green corn and as a cereal for brewing, to have them growing types of maize which are similar to each other yet rare or unknown in the New World puts the burden of proof on any one who would ascribe all this development to separate post-Columbian acquisitions.

It seems more likely that there have been at least two major movements of maize in Asia. The latter in early post-Columbian times brought what is essentially a Caribbean type of maize to the Philippines and to many countries actively colonized by the Europeans. Back in the hills, however, are much more primitive types, unaggressive, not particularly productive, grown by conservative people. If one asks why they did not spread more the answer is that they did spread in Asia from Persia to Sumatra and New Guinea, which is virtually as far as the Asiatic *Sorghum* (which was their companion crop) has been carried.

The general evidence for the main kinds of maize in South America and in southeast Asia is crudely and diagramatically summarized in fig. 2. The letters *A*, *B*, and *C* represent three of the major races which make up *Zea Mays*. Letters within parentheses indicate that a particular type is present but is relatively uncommon. Each of these major races has a core of morphological characters in common in spite of great variation from variety to variety within the race (Anderson and Cutler, 1942). *A* represents the small-kernelled types we have just been describing and mixtures with them. In South America they are found today either as rare native popcorns or as one of various primitive tendencies in the highly heterozygous maize of the eastern river basins (Cutler, 1946). In Asia they are practically confined to hill areas and in the most isolated are the only type. In western South America, where we have stratigraphic archaeological evidence, we know that race *A* was for centuries the only type of maize. *B*, in fig. 2, represents the distinctive large-seeded frequently large-cobbed types of the Andean region, which are practically exclusive at higher altitudes, which have dominated (at least in mixtures) the west coast ever since prehistoric times (late Ica) and which are one of the elements in the maize of the Amazon basin. Such types are apparently unknown in Asia, a most significant fact. *C* stands for the widely adaptable types of the Caribbean basin which spread so rapidly and extensively around the world in post-Columbian times.

This diagram is factual and though some of these facts are matters of judgment; with other types of maize it has already proved possible to make objective records of such racial differences (Anderson, 1944; Brown and Anderson, 1947; and Anderson, 1947), thus taking such questions out of the realm of acrimonious quibbling. The interpretation of these facts is quite another matter. The facts are in themselves fantastic; any satisfying hypothesis must border on the miraculous. One fact seems to be clear. Race *C*, which we know to be archaeologically post-Columbian in South America, was widely spread in post-Columbian times. If we therefore remove *C* from consideration, the problem to be solved is how could race *A* get to a number of isolated hill areas in Asia without anywhere leaving a very definite record along the coast of Asia? If, for the sake of argument, we grant that it might somehow have spread there from the Upper Amazon in post-Columbian time, who brought it and how? Was there somewhere in the New World a reservoir of various *A* varieties which has since disappeared? Could all the *A* varieties in Asia have differentiated themselves in all these backward areas into a set of unique but similar varieties under the stimulus of a new environment? These are possibilities but they certainly seem fantastic.

If we admit (with a growing minority of archaeologists) the possibility of trans-Pacific contact in very early pre-Columbian times, then race *A* might have crossed the Pacific at an early date when maize was still an unaggressive little popcorn, to be carried across the Pacific again when the dominant world crop which we now know had been developed in the New World. As to which way maize made its first crossing, whether from Asia to the New World, or *vice versa*, the facts of fig. 2 do not even suggest an hypothesis. From the generally accepted facts as to the relationships of maize a good case could be made out for either Asia

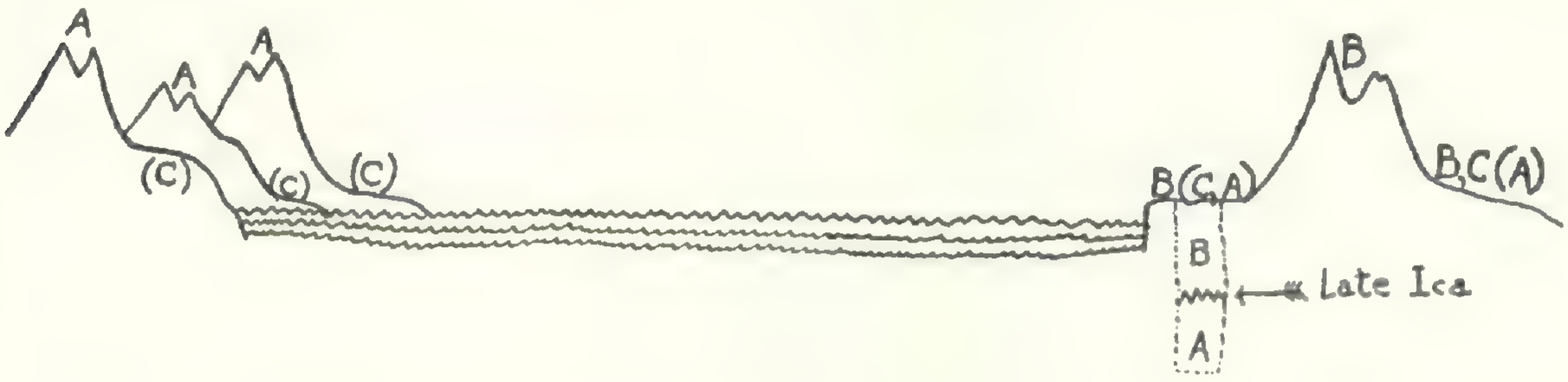


Fig. 2. Distribution of the major races of maize in South America and in Asia. Very diagrammatic, *A*, *B*, and *C* represent three of the main kinds of maize, each consisting of various sub-races and innumerable varieties. Though these races may intermingle, each has its own core of correlated tendencies: Race *A*, archaeological and Asiatic—small ears, large glumes, subspherical seeds, short internodes, drooping and included tassel, green plant color; Race *B*, Andean—large kernels, pineapple-shaped ears, large cobs, strong plant color; Race *C*, tripsacoid—long ears, stiff tassel, bony cob. Letters in parentheses indicate areas where a particular race is known only in mixtures with other races. In the Orient race *C* is represented in "Caribbean Flints" a mixture of *C* and other races. Asia is diagrammed to the left of the figure, South America to the right, with the Pacific in between. For western South America there is extensive archaeological evidence, some of it stratigraphic, which allows us to establish a sequence of maize types from *A* to *B*.

or the New World as a primary center. There can be no doubt that the New World was certainly the secondary center, or rather a whole set of secondary centers.

The physical possibilities of transfer by the early Polynesians are much more likely than most botanists are aware. These early people were skilled navigators who could deliberately set out for Hawaii from Samoa and arrive at Hawaii. Furthermore, they were skilled cultivators who carried vegetatively propagated varieties of various crops to many of the islands of the Pacific (Buck, 1938). Getting the improved taro and bread-fruit to Hawaii (which they are known to have done) would have called for more skill as navigators and cultivators than to have taken maize from New Guinea to Peru.

Nor would maize have been exceptional among cultivated plants had it been taken across the Pacific. It is known that the gourd crossed the Pacific in very early pre-Columbian times and it is admitted by most authorities that the cultivated sweet-potato originated in the New World but spread in pre-Columbian times to Polynesia and even as far as New Zealand. The sword bean *(Canavalia)*, widely cultivated throughout the Pacific and always considered to be of Old World origin, is now known from prehistoric sites along the coasts of both South America and Mexico.

The hypothesis here suggested as to the origin and developments of maize is paralleled almost exactly by the conclusions concerning cotton reached after long cooperative research by the British cotton experts (Hutchinson, Silow & Stephens, 1947). In the case of cotton, polyploidy operated to keep certain mixtures of old and New World germ-plasm from losing their identity in the mixture, thus making the story quicker to untangle and more difficult to controvert.

For many minor domesticated plants, the rather complete neglect of cultivated plants and weeds by taxonomists leaves any general discussion of the problem at the stage of mere guesswork. Neither the cotton story nor that of maize could be put together until a beginning had been made at the fiendishly difficult problem of classifying and cataloguing their various cultivated varieties. Both Amaranths and Chenopodiums are cultivated by the hill peoples of Asia and of the New World as cereal crops, pot-herbs, ornamentals, magic plants, and food colors. Not until these groups have been meticulously collected and monographed (the cultivated strains, the weeds, and the genuinely wild entities) can we be in a position to discuss the evidence. Similar careful studies are needed of the various strains of *Bixa Orellana*, of Job's tears *(Coix)*, of *Pachyrhizus*, all of which are widely distributed in both the Old World and the New. There is little really critical taxonomic evidence on origin and diffusion for any of these groups at present. It is disappointing to find, half-way through the twentieth century, that our botanical evidence is not yet at a stage where such fundamental questions can be authoritatively discussed. For the plants most directly associated with man, the cultivated plants

and weeds, aside from a few collections by such pioneers as Ames, L. H. Bailey, and Merrill, we do not have the specimens let alone the critical studies. The average botanical collector is so intrigued by cloud forests and river jungles that he does not even think about the more difficult problems posed by the vegetation of dump-heaps, clearings, and cultivated fields.

For maize itself, two facts suggest how complicated a story may be involved: (1). The relationship of *Sorghum,* Assamese maize, and prehistoric North American maize. Whatever the explanation, it is clear that the maize of Assam is more like *Sorghum* in a number of different ways than is any other modern maize as yet examined in detail. Whatever the explanation, it is also clear that the earliest prehistoric maize cob described from Bat Cave, New Mexico, by Mangelsdorf and Smith (1949) is even more *Sorghum*-like in the details of its inflorescence, while cobs from the upper layers of the same cave are as radically un-*Sorghum*-like as it is possible for maize inflorescences to be. It may be that maize and *Sorghum* have had a parallel evolution in the Orient under the stimulus of a similar set of environments. It may be that they are related in some way; it is known that they have the same chromosome number. Whatever the explanation, the whole story must be a complicated one. (2). Much of the maize of Central and North America has knobs on its chromosomes, a character which Mangelsdorf and Reeves ascribed (1939) to introgression from *Tripsacum,* a New World grass. Much of the maize of South America is knobless. The maize of Assam has only a few knobs but they are frequently quite large and they tend to occur at positions and in combinations which are either rare or unknown in New World maize. Here again a complicated history of exchange and evolution is suggested.

Only one thing is certain. We must have extensive and critical collections of Oriental maize if we are to understand *Zea Mays* and utilize it most effectively. We need this information for practical and theoretical purposes. Kuleshov (loc. cit.) describes and illustrates dwarf, drought-resistant types from Persia. Larroque tells (personal communication) of a small-grained sort raised in Indo-China for chicken feed which germinates effectively in the soaking wet soil of rice paddies. More important and far-reaching is the need for such collections if we are to understand the history of maize. Along with *Drosophila* and *Neurospora,* the science of Genetics is built on work with *Zea Mays.* The brilliant work of Stadler and of McClintock, for instance, might have quite different implications for the fundamental nature of evolution or for the protein chemistry of the germ-plasm, depending upon the actual history of the germ-plasm which they have been using, the germ-plasm of *Zea Mays.* Certainly we cannot even discuss the probable history of *Zea Mays* in an intelligent fashion until we have at least an approximate notion of what varieties of maize are being grown by the Lolo in central Asia, by the hill tribes of Burma, Siam, and Indo-China, by the aboriginal remnant in Hainan and Formosa, and in the isolated interior of New Guinea.

GENERAL SUMMARY

Part I:—

1. The various hill tribes of Assam and neighboring regions are enumerated and their relationships to each other and to outside peoples are briefly described. In general, these tribal peoples grow their own food, weave their own clothing, and regulate their own affairs by tribal law. They have no writing and their religion is animistic.

2. The varieties and uses of maize are enumerated tribe by tribe. It is used for human food, particularly when immature (i.e., as "green corn"), for beer-making, as popcorn, and for pig-feeding. Its importance varies from tribe to tribe but, along with the cereal forms of Job's-tears *(Coix)* and millet *(Sorghum)*, it is traditionally one of the ancient foods of the region.

3. It is usually grown in lines or patches or as single plants among other cereal crops. In spite of this practice, the varieties are kept remarkably pure, even when five or six distinct types are grown by a single village.

4. The wide distribution in the area, the traditions and positive statements of the peoples themselves, the existence of tribal names, and the place of maize in their religions all point to a long history in this region, going back for centuries at least and most probably antedating rice culture there.

Part II:—

1. The assembling of all the evidence on the morphology of these Assamese varieties was a complicated affair, because their growing season is long and because the importation of maize from southeastern Asia is necessarily restricted[1]. They were collected directly from the Naga and grown in duplicate in Assam and California. A set of the original ears was photographed on the ear in London, and plants from ear-to-row tests were photographed in California and in Assam. Pachytene smears were made of many of the cultures, and a few of the original cobs were studied in celloidin section by Lenz.

2. There are considerable differences between the Assamese varieties (most of which are remarkably uniform within the variety). As a whole they tend to have: slight or no plant color, many short internodes, semi-included tassels, spathe-like upper leaves, pendent tassel branches, several small ears, long slender leaves, short silks, dull aleurone colors, small subspherical kernels. They are outstanding, both in Assam and in this country, for their lack of vigor.

3. This complex of characters is unknown in Mexico and Central America. In South America it is approached only in mixtures from the eastern rivers and in certain primitive popcorns. In prehistoric times, varieties with similar cobs and kernels were the only type of maize along the west coast of South America for a very long period.

---

[1] Due to the presence of two of the world's worst maize diseases in this area, in itself a significant fact.

4. The distribution of these and similar varieties in the Orient is reviewed. They are widely though spottily distributed from Persia and Turkestan to Tibet and the Island of Hainan, nearly always among primitive and conservative peoples.

5. It is concluded that there have been at least two major movements of maize in Asia. The later one, in early post-Columbian times, brought what is essentially a Caribbean type of maize to the Philippines and to many of the countries actively colonized by the Europeans. Back in the hills, however, are more primitive types whose progenitors must have crossed the Pacific in pre-Columbian times, though in which direction (or directions) the evidence does not indicate.

6. The possibility of trans-Pacific transfer of a primitive and unaggressive race of maize by early Polynesians is discussed. It is shown to parallel the conclusions reached by the most recent workers on cotton. For the study of such problems, the imperative need of more critical taxonomic evidence on cultivated plants and weeds is discussed and illustrated by examples.

7. It is concluded that maize has had a long and complicated history. As a dominant crop it certainly developed in the New World. As a primitive, relatively unproductive crop, utilized for brewing, for popping, and for green corn, it is almost universal among the primitive peoples of central and southeastern Asia. Presumably it must either have originated in Asia or have been taken there in pre-Columbian times. Before we can discuss the history and origin of maize intelligently we shall need an approximate survey of the kinds of maize being grown by these peoples.

BIBLIOGRAPHY

Anderson, Edgar (1943). A variety of maize from the Río Loa. Ann. Mo. Bot. Gard. **30**:469–474.

————, (1944). Maíz reventador. *Ibid.* **31**:301–312.

————, (1946). Maize in Mexico. *Ibid.* **33**:147–247.

————, (1947). Corn before Columbus. 24 pp. Des Moines, Ia.

————, and William L. Brown (1947). The northern flint corns. Ann. Mo. Bot. Gard. **34**:1–22. *pl. 1–6.*

————, and H. C. Cutler (1942). Races of *Zea Mays*. I. Their recognition and classification. *Ibid.* **29**:69–86.

Buck, Peter H. (1938). Vikings of the Sunrise. New York.

Collins, G. N. (1909). A new type of Indian corn from China. U. S. Dept. Agr. Bur. Plant Ind. Bull. 161:1–30, *pl. 1–2.*

————, (1920). Waxy maize from Upper Burma. Science, N. S. **52**:48–51.

Cutler, Hugh C. (1946). Races of maize in South America. Bot. Mus. Leafl. Harv. Univ. **12**:257–291.

Emmons, Ebenezer (1849). Agriculture of New York **2**:263–265. Nat. Hist. N. Y. Pt. V, Vol. 2.

Von Fürer-Haimendorf, Cristoph. (1939). The Naked Nagas. 243 pp. London.

Hutchinson, J. B., R. A. Silow, and S. G. Stephens (1947). The evolution of Gossypium. 160 pp. Oxford Univ. Press.

Kuleshov, N. N. (1928). Some peculiarities in the maize of Asia. Bull. Appl. Bot. and Pl. Breed. **19**:325–374.

————, (1929). The geographical distribution of the varietal diversity of maize in the world. *Ibid.* **20**:506–509.

————, (1930). The maize of Mexico, Guatemala, Cuba, Panama, and Colombia. *Ibid.* Suppl. 47:492–504.

Laufer, B. (1907). The introduction of maize into eastern Asia. Cong. Int. des Americanistes. pp. 223–253. Quebec.

Lenz, L. W. (1948). Comparative histology of the female inflorescence of *Zea Mays* L. Ann. Mo. Bot. Gard. **35**:353–376.

Mangelsdorf, Paul C., and R. G. Reeves (1939). The origin of Indian corn and its relatives. Texas Agr. Exp. Sta. Bull. 574.

———, and C. Earl Smith, Jr. (1949). New archaeological evidence on evolution in maize. Bot. Mus. Leafl. Harv. Univ. **13**:213–247.

Merrill, E. D. (1941). Man's influence on the vegetation of Polynesia with special reference to introduced species. Proc. Sixth Pacific Cong. **4**:629–639.

Explanation of Plate

PLATE 18

Fig. 1. Monba tribe. Threshing maize, Dirang village. (November, 1946).

Fig. 2. Monba tribe. Maize stacked for ripening, Pakung village. (November, 1948).

1

2

STONOR & ANDERSON—MAIZE OF ASSAM

Explanation of Plate

PLATE 19

Fig. 1. Eastern Dafla tripe. Carrying in the maize from the fields. (November, 1946).

Fig. 2. Lhota Naga tribe. Corner of a "jhum" field, with lines of maize growing among the rice. (May, 1947).

1

2

STONOR & ANDERSON—MAIZE OF ASSAM

Explanation of Plate

PLATE 20

Three views of Stonor No. 13 (Early Slender). Scale indicated by the lines in the background which were originally spaced at 50 cms. Below: habit of plant when tassel began to shed pollen. Note the "spathe" of upper leaves which is directed towards the camera. Upper left: the same, viewed from the side. Upper right: close-up of tassel after pollen shedding was complete. Note proximity of upper leaf to base of tassel. Photographs courtesy of California Institute of Technology.

STONOR & ANDERSON—MAIZE OF ASSAM

Explanation of Plate

PLATE 21

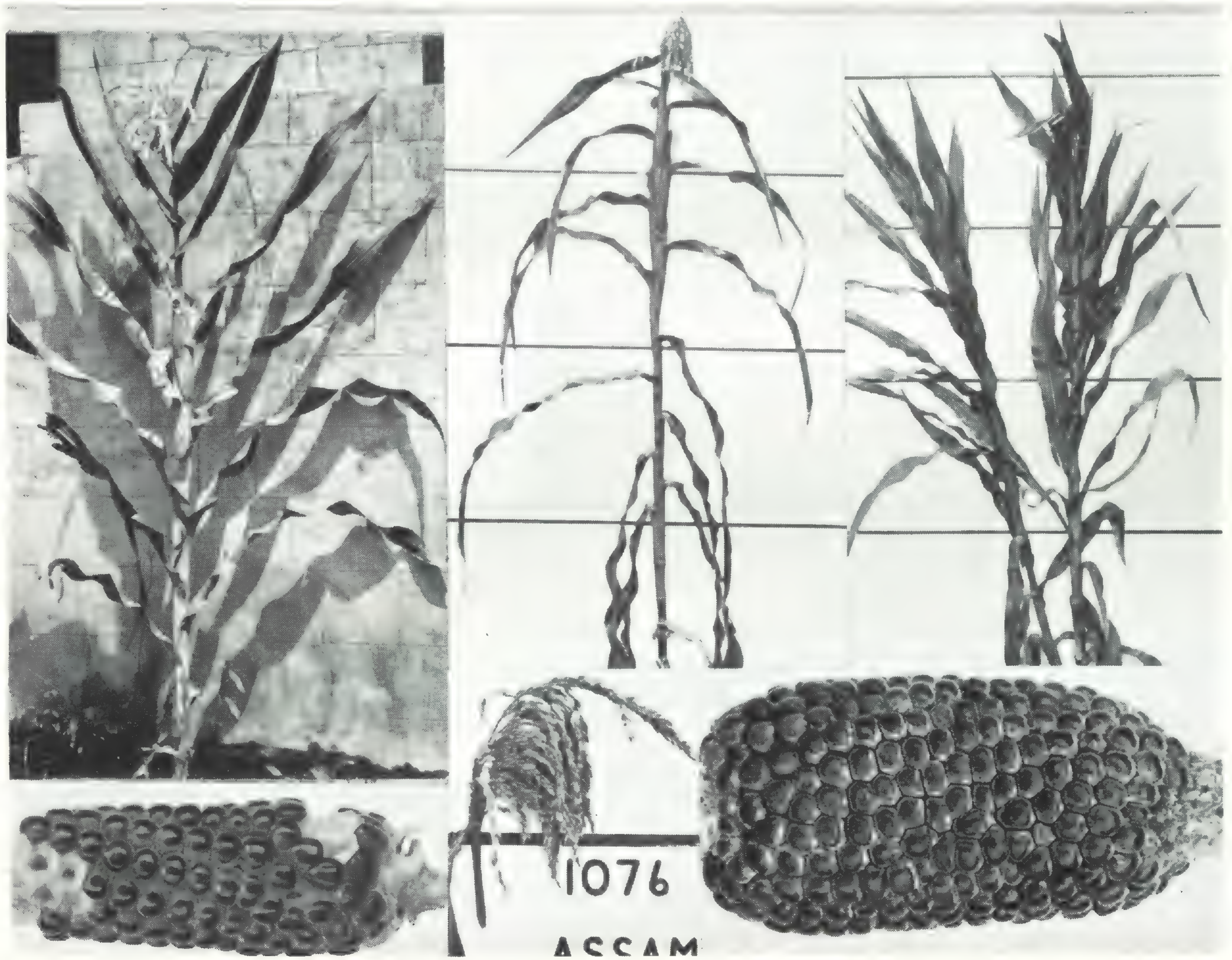
Lower left: habit of Stonor No. 16 (Drooping Waxy). Scale indicated by the lines in the background, originally spaced at 50 cms. Note clustering of upper leaves due to short internodes. Tassel had been shedding for some time and was nearly mature when the photograph was taken. Photograph courtesy of California Institute of Technology. Right: ear of Stonor No. 18 (Late Sidewise). Approximately natural size. Above: portion of ear No. 13, approximately natural size. Photographs of ears, courtesy of Royal Botanic Gardens, Kew, England.

STONOR & ANDERSON—MAIZE OF ASSAM

Explanation of Plate

PLATE 22

Ears and plates of Late Upright and Early Upright. Upper left (with stone background), photograph of Stonor No. 8, taken in Shillong, Assam. Note erect and ribbed leaves, still slightly twisted, and that ears scarcely extend from the axils of the leaves. Center above: Stonor No. 5, photographed at a slightly later stage just as the silks were beginning to wither and after all the pollen had been shed. Note that tassel is not completely exserted from upper leaves and that mature ears scarcely exceed their subtending sheaths. Center below, tassel of same plant with its uppermost leaf. Upper right: Stonor No. 6, habit just as tassel was beginning to shed pollen. Note tassel practically hidden by the upper leaves, which are twisted, upright, and ribbed. Scale in this and previous two figures indicated by lines which were originally spaced at 50 cms. Photographs courtesy of the California Institute of Technology. Lower right: ear of Stonor No. 8; lower left: ear of Stonor No. 6, both a little less than natural size. These two ears are almost identical with the popcorns found in early prehistoric graves in coastal Peru (Paracas, Cañete, etc.). Photographs of ears courtesy of Royal Botanic Gardens, Kew, England.



STONOR & ANDERSON—MAIZE OF ASSAM

STAFF
OF THE MISSOURI BOTANICAL GARDEN

Director
GEORGE T. MOORE

HERMANN VON SCHRENK,
Pathologist

JESSE M. GREENMAN,
Curator Emeritus of the Herbarium

CARROLL W. DODGE,
Mycologist

EDGAR ANDERSON,
Geneticist

ROBERT E. WOODSON, JR.
Curator of the Herbarium

HENRY N. ANDREWS,
Paleobotanist

ROBERT W. SCHERY,
Research Associate

GUSTAV A. L. MEHLQUIST,
Research Horticulturist

ROLLA M. TRYON,
Assistant Curator of the Herbarium

GEORGE B. VAN SCHAACK,
Honorary Curator of Grasses

JULIAN A. STEYERMARK,
Honorary Research Associate

NELL C. HORNER,
Librarian and Editor of Publications

GERALD ULRICI,
Business Manager

BOARD OF TRUSTEES
OF THE MISSOURI BOTANICAL GARDEN

President
RICHARD J. LOCKWOOD

Vice-President
DANIEL K. CATLIN

Second Vice-President
EUGENE PETTUS

L. RAY CARTER
DUDLEY FRENCH
HENRY HITCHCOCK
JOHN S. LEHMANN
GEORGE T. MOORE
A. WESSEL SHAPLEIGH
ETHAN A. H. SHEPLEY

EX-OFFICIO MEMBERS

ARTHUR H. COMPTON,
Chancellor of Washington University

JOSEPH M. DARST,
Mayor of the City of St. Louis

WILLIAM P. GRUNER,
President of the Academy of Science of St. Louis

WILLIAM SCARLETT,
Bishop of the Diocese of Missouri

WILLIAM SCHUMACHER
President of the Board of Education of St. Louis

GERALD ULRICI, *Secretary*

Volume XXXVI Number 4

Annals
of the
Missouri Botanical
Garden

NOVEMBER, 1949

On Some Uses of Maize in the Sierra of Ancash . . . . . Charles M. Rick and Edgar Anderson 405–412
Spores of the Genus *Selaginella* in North America North of Mexico . . . . . Alice F. Tryon 413–431
The Cytology of *Paphiopedilum Maudiae* Hort . . . . . Henry A. McQuade 433–472
Stegnosperma: A New Species and a Generic Commentary . . . . . David J. Rogers 475–477
Nucellangium, A New Genus of Fossil Seeds Previously Assigned to *Lepidocarpon* . . . . . Henry N. Andrews, Jr. 479–504
A Revision of the Genus *Heliocarpus* . . . . . KoKo Lay 507–541
New Apocynaceae of South America . . . . . David de Azumbuja and Robert E. Woodson, Jr. 543–548
General Index to Volume XXXVI 551–554

PUBLISHED QUARTERLY AT GALESBURG, ILLINOIS,
BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN,
ST. LOUIS, MISSOURI.

Entered as second-class matter at the post-office at Galesburg, Illinois,
under the Act of March 3, 1879.

Annals

of the

Missouri Botanical Garden

A Quarterly Journal containing Scientific Contributions from the Missouri Botanical Garden and the Henry Shaw School of Botany of Washington University in affiliation with the Missouri Botanical Garden.

Information

The ANNALS OF THE MISSOURI BOTANICAL GARDEN appears four times during the calendar year: February, May, September, and November. Four numbers constitute a volume.

Subscription Price	$10.00 per volume
Single Numbers	2.50 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

Annals
of the
Missouri Botanical Garden

Vol. 36 NOVEMBER, 1949 No. 4

ON SOME USES OF MAIZE IN THE SIERRA OF ANCASH

CHARLES M. RICK[1] AND EDGAR ANDERSON

In its long association with man, maize has had a complicated career. It has been used by various peoples and in various ways. One might compare its whole history to a complex fabric, its warp the multitudinous varieties of this versatile crop, its woof the myriad uses to which *Zea Mays* has been put by the peoples who have grown it. In interpreting and understanding this history and in developing the broadest use of this world asset, one can never predict which of these various strands will be most useful in unravelling some particular problem. One finds ethnological curiosities leading to modern technological progress; for example, waxy maize, developed by Asiatic aborigines (Collins, 1909), became the clever solution to wartime shortages of industrial carbohydrates (Sprague and Jenkins, 1948). In reporting these rather unusual uses of maize in the South American highlands we would not venture to predict whether their greatest significance might be to an historian, a biochemist, an archaeologist, a plant breeder, or to some imaginative industrialist.

Ancash is a small department including part of the Coast and Sierra of Peru north of Lima. It is largely drained by the Río Santa, one of the largest rivers of the western slopes of the Peruvian Andes. Throughout most of its length the Santa is flanked on the west by the Cordillera Negra and on the east by the Cordillera Blanca, the latter completely dominating the scenery of Ancash with its chain of very high peaks and their glaciers and perpetual snowfields. Excepting its upper and lower extremities, the large trough between these two ranges is known as the Callejon de Huailas *(sensu latu)*. The Santa varies in elevation in this region from 3,370 m. at Recuay to 2,150 m. at Villa Sucre (Weberbauer, 1945). Sugar cane and other tropical and subtropical crops are cultivated under irrigation in the lower reaches, maize and small grains in the upper part, the latter

[1]College of Agriculture, University of California, Davis; Fellow, John Simon Guggenheim Memorial Foundation, 1948-49.

crops being irrigated in the few areas in which the ground is reasonably flat and in which water is accessible. On the higher slopes, up to 4,300 m., pastures, potatoes, barley, fava beans, and other crops are grown without irrigation. Maize and other crops dependent upon rainfall are grown in the rainy season from October to May.

The Callejon de Huailas is one of the most populated valleys of the Peruvian Sierra. The great majority of the people are pure-blooded Indians or descendants of Indians. They live in the larger centers, in small outlying villages, or in solitary dwellings in the fields. Typical of the Peruvian Indians, they live according to the same primitive customs that their forbears have followed for centuries, almost without modification by contact with modern civilization. As a closely knit group, however, they differ in varying degrees from the *serranos* of other sections: they dress in their own characteristic costumes; their *quechua* language is greatly modified; and they deviate in certain uses of food plants. Much of the commerce and agriculture of the region is managed by a small group of pure whites, or nearly pure whites, whose life is influenced to a surprising extent by the Indians with whom they live. This influence is evident in their language and foods.

Part of the information for this publication was gathered by the senior writer from informants and from observations made during a stay of two weeks in January, 1949, in the Callejon de Huailas. We are deeply indebted to Señora Elola Haro de Guzmán, our chief informant, who offered generous hospitality and answered innumerable questions with utmost patience and understanding. She has always lived in the vicinity of Huaráz, capitol of the department of Ancash. From the time of her husband's early death, some 20 years ago, she has personally managed the affairs of the family farm or *chacra,* in which, like many Peruvian *chacras,* the Indian laborers live and work in what might be called a benevolent sharecropper basis. Through this experience and her many other contacts with people in the area, Señora de Guzmán has become thoroughly versed in the life of the Ancash Indians.

Maize, the most important food plant in the Sierra of Ancash, is used in a great variety of recipes. The most unusual use of maize and one which apparently is not known outside Ancash is *tocos de maíz* or fermented maize.

Tocos—The most popular maize variety for the preparation of tocos is *cusqueño blanco,* a variety typically having eight-rowed ears of enormous grains with soft floury endosperm. If *cusqueño blanco* is lacking, other white-grained varieties are used. The maize is used only in the mature state.

The fermentation or rotting process is conducted in the following fashion. The whole ears, husked, but with grains still attached, are placed in any quantity in a sack of linen (wool or cotton cannot be used presumably because they would disintegrate in the process). The sack is tied shut securely and is submerged in water in a hole that has previously been dug in an irrigation ditch where the water is flowing freely. The hole must be deep enough so that the sack and its contents are covered by at least two inches of water. Stones are placed on top in order to

prevent the sack from rising above water. Aside from the importance of keeping the sack submerged, the depth of submergence does not seem to matter. A very important part of the process is to place the stones and to arrange the surrounding ground and grass so that the cache cannot be readily detected. *Tocos* are very popular and therefore valuable items of commerce, and their loss by theft is by no means uncommon.

The maize can also be fermented in large pools of standing water, but it is considered that a product of better quality is produced in running water. Whether the water is standing or running it is essential that the maize be completely submerged in water in a hole in the ground.

Whatever changes occur, the fermentation must be anaerobic or semianaerobic. The length of time required for the process depends on the age of the maize and probably also on the temperature of the water. When recently harvested ears are used the fermentation is complete in two months, but if the ears are older and the grains harder it may be necessary to wait as long as three months. The stage of fermentation is determined by touch, the process being completed when the grains are soft, at which stage they are bloated and have a somewhat water-soaked appearance.

When the desired stage of fermentation has been reached, the pericarp is removed from the grains, which still remain on the ear, by rubbing with the fingers. It is not possible to do this before the fermentation is completed. The ears are then washed in cold running water. They are washed well, but gently, so that none of the starch is lost.

At this stage the *tocos* are ready for cooking and can be stored in a moist condition for no more than seven or eight days. If it is desirable to keep them for a longer period, they are dehydrated in the sun. The grains are shelled from the ears and are spread thinly in a place where they will receive the maximum amount of sunlight. Depending upon the light intensity, from four days to two weeks are required to complete the dehydration. If the grains are well dried they can be stored for one or two years under the generally cool household conditions of the Sierra. Fresh *tocos* are considered to make a better product than dried ones. They are marketed in both forms.

The usual cooking process consists of stewing them in an *olla*, or low earthenware pot with a mouth nearly as large as the largest diameter. The *tocos* are placed in the *olla* and enough boiling water added to cover them. Either refined cane sugar or *canchaca*, a crude brown sugar considered to be superior to refined sugar for this purpose, is added, the amount depending upon taste. Sugar is required to offset the natural acidity of the product. Sometimes herbs are added for flavoring, but the uses and purposes of these are not well understood and are said to be secrets of the Indians. The mixture is cooked for 20 or 30 minutes.

The odor of this dish, which is not the least bit dissipated by cooking, is reminiscent of vases of flowers in which the water has not been changed often enough. It is just barely possible for the uninitiated to stay in the same room when

tocos are served. They are much more agreeable to taste than to smell, according to the experience of the senior writer. They are eaten in great quantities without ill effect and are very popular both among Indians and whites of the region. They are probably no more offensive to us than our sauerkraut or highly scented cheeses would be to the Ancash Indian. It is conceivable also that certain valuable vitamins, possibly of the B complex, might be elaborated in the rotting process.

Tocos are generally eaten for lunch and dinner, but there is no great regularity, they being consumed also at other hours of the day. They are served warm like a stew, but are also very popular chilled after cooking. They are considered effective as a remedy against colds. There is no distinction as to age of the person eating *tocos* or occasion on which they are served. In the recollection of Señora de Guzmán they have retained a constant popularity in her time.

In the Sierra of Ancash possibly 20 per cent of the maize is consumed in the form of *tocos*. More extensive use is probably limited because they are more difficult to prepare than other maize foods. Yungay (2,535 m.) and Carhuas (somewhat higher elevation) in the Callejon de Huailas are the principal centers of preparation of *tocos*. From these centers they are transported to other markets in Ancash. Because they are in brisk demand, they sell rapidly whenever offered. The reasons for the development of this use in these places is not well understood. Climatic conditions can hardly be responsible for the restriction to Yungay and Carhuas because *tocos* of good quality can be prepared at Huaráz, which lies at a considerably higher elevation (3,080 m.).

We inquired extensively in both the Sierra and Coast of Peru, but found no evidence of the use, and very little evidence of the knowledge of *tocos* outside the Sierra of Ancash. Informants would nearly always indicate familiarity with *tocos* upon inquiry and upon mention that it was a fermented maize product, but further questioning would generally reveal that they were thinking of *chicha* or some other product and that they had never actually heard of *tocos*. It is impossible to state the antiquity of this use of maize. Since it is used universally by the Indians of Ancash and since it is known only by a name in the *quechua* language, it seems likely that its use antedates the colonial period.

We are indebted to Dr. Carl O. Sauer, of the Department of Geography, University of California, for calling our attention to the following quotation from the works of de Champlain, which leaves no doubt that a similar product was used by the Huron Indians:

> They have another way of eating Indian corn, to prepare which they take it in the ear and put it in water under the mud, leaving it two or three months in that state until they judge that it is putrid; then they take it out and boil it with meat or fish and then eat it. They also roast it, and it is better that way than boiled, but I assure you that nothing smells so bad as this corn when it comes out of the water all covered with mud; yet the women and children take it and suck it like sugar-cane, there being nothing they like better, as they plainly show.—[Biggar, 1929, 3:129–130.]

A similar product, *tocos de papa,* is prepared from a potato variety called *anco* having rather dry white flesh. Methods of fermenting and even of drying the fermented tubers are almost identical to those used for maize.

According to Señora de Guzmán *tocos* have a medicinal value in addition to their putative value in curing colds. They are used in the following manner to cure filmy eye of the burro or horse. Dehydrated *tocos de papa* are finely ground and passed through a fine screen. The fine powder thereby obtained is blown into the infected eye through a small tube of paper.

Cancha—In the vicinity of Huaràz this name applies to parched maize, but in other parts of Peru it appears to be a general term pertaining to both parched and popcorn. Even in its restricted use to parched corn, it is by far the most popular form of prepared maize in the Callejon de Huailas. Perhaps 50 per cent of all the corn in the Sierra of Ancash is used as *cancha.* Almost any form of maize can be used for *cancha,* but *tercio pelo* or *maíz dulce,* a variety having starchy, hard, rounded grains of reddish brown color with a yellow tip, is preferred. Another variety, *pacchus,* apparently a true sweet corn, is also considered satisfactory for this use.

For the preparation of *cancha* (and probably also popcorn) the Indians of Ancash use a baked clay vessel called the *tiesto,* which is mound-shaped and slightly rounded on the bottom. It has a small opening on the side and may or may not have a handle. They are generally 20–30 cm. in diameter.

Valcárcel (1934) described and illustrated a similar vessel that was unearthed in the ruins of Sacsahuamán (department of Cuzco). This specimen or one very similar to it was seen by the senior writer on a visit to the Instituto Arqueológico

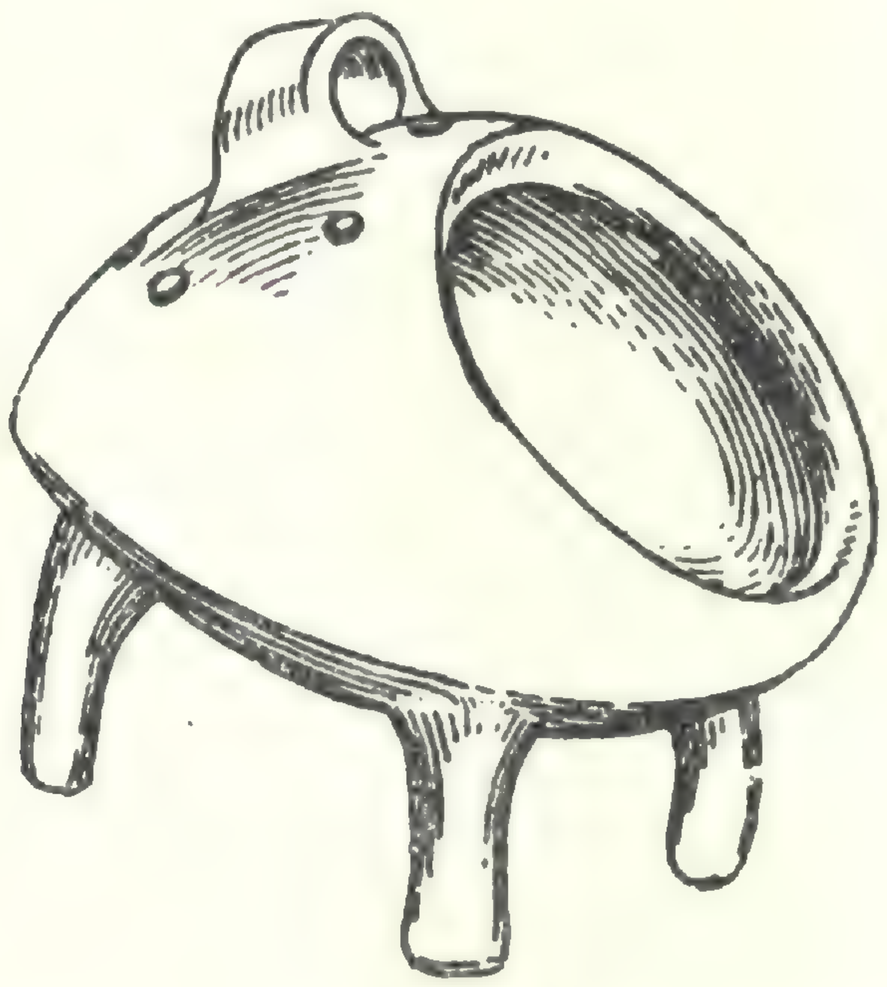


Fig. 1. *Olla canchera,* a prehistoric vessel used to parch maize. Reproduced from Valcárcel (1934).

del Cuzco and is copied by photostat from the cited paper as the accompanying fig. 1. Valcárcel describes it as follows (p. 228):

> 1–408—Olla canchera tripode de barro cocido. Con asa. Sin pulir y sin ornamentar. Lleva seis perforaciones cerca del asa y tiene la base ennegrecida probablemente por el fuego. Factura semifina. Por lo diminuto de su tamaño parece juguete, réplica de otros mayores. Alto 6.2 cm. Diam. de la boca 3.7 cm., Diam. de la base 6.2 cm. (Vessel of fired clay with three legs, used for preparing cancha. With handle. Without polish or ornamentation. It has six holes near the handle and its base is blackened, probably by fire. Semifine artefact. For the smallness of its size it appears to be a toy, a replica of other larger ones. Height 6.2 cm., Diameter of mouth 3.7 cm., Diameter of base 6.2 cm.)

Another example described as a brazier or small stove was illustrated by Bingham (1930). This artefact, dug from the ruins of Machu Picchu, closely resembles the preceding one in shape, but is larger, being 17 cm. high. In his more recent book, 'Lost City of the Incas' (1948), one is illustrated opposite page 42, where it is described (erroneously, we suspect) as "A Brazier for Annealing Bronze Articles."

The *tiestos* of Ancash resemble these precolumbian *ollas* in general shape except that they have smaller mouths, lack the legs, and may or may not have the handle. The hooded form of these vessels prevents the escape of grains that jump during the parching. The senior writer has also seen *cancha* prepared in Huaráz in open earthenware vessels having the general shape of our frying pans.

To prepare *cancha* only mature grains are used. These are placed without other ingredients in a *tiesto* that is heated as hot as possible over a wood or charcoal fire. The grains are soon toasted and slightly expanded by the heat. After they have reached this stage the grains are removed and cleaned on paper or cloth. They may be flavored with melted lard and salt. A supply of *cancha* is usually not kept for more than one day. Two batches—one in the morning and another in the afternoon—are usually prepared per day.

Cancha is immensely popular in Ancash and throughout the Peruvian Andes. The parched grains may be eaten at any time of the day and at all times of the year. Everyone, children included, eat it. It is very convenient for the worker to carry a pouch of it with him at all times and to crunch away on the grains whenever hungry. When *cancha* is lacking in a household, it is bought in the market or from a neighbor. It is veritably "*el pan de los indios mejor dicho.*" In Ancash *cancha* is not ground to prepare a flour. The only type of *arina* or flour that is prepared from maize is ground from untreated grains or from *chochaca.*

Chicha—This mildly alcoholic beer-like drink is by far the most important beverage of the Sierra. We are aware of several methods of preparation, but we did not investigate in detail the processes employed in Ancash since they are similar to the well-known methods of the Peruvian Sierra. Methods of preparing *chicha* in various sections of Bolivia are described in detail by Cutler and Cárdenas (1947).

Chicha de jora, considered the *chicha* of best quality, is prepared from malted maize. Grains of several different yellow or red varieties are sprouted and then

dried. The grains are stored or marketed in the dried sprouted condition. These are ground and mixed with water in large earthenware jars for fermenting.

Chicha morada, another well-known product, is prepared from the maize variety known as *morada* having dark purplish grains and cobs. The dried grains are ground and the consequent flour is stewed with the cobs in water. The mixture is filtered and allowed to ferment.

Other *chichas* are prepared from barley, wheat bread, fava beans, and other crops in Ancash.

Mote—This is a form of hominy prepared from mature grains of preferably a white variety of maize. The grains are treated in a boiling lye solution *(lejía)* prepared from water and ashes, for one-half hour. The pericarp is then removed and the grains are boiled further until they burst. *Mote* is eaten in this form or is ground for the preparation of *masamoras* (puddings) or *tamales*. *Mote*, like *tocos*, can be dehydrated for storage.

Chochaca—Mature grains are shelled from the ear and cooked in a great quantity of water until they split slightly. The grains are then spread in the sun to dry and are stored for whatever time they might be needed. The drying process is facilitated by first exposing the grains to frost on a cold night before spreading them in the sun. *Chochaca* is used mostly for soups, for which purpose it is ground.

One might point up this picture of maize in these remote highlands by contrasting it with maize in the United States where it is primarily our medium for producing the maximum amount of beef and bacon per man hour per acre, and secondarily a most delicious vegetable. Or contrast either of these with uses in Mexico where it is indeed the immediate staff of life for nearly every citizen and ordinarily is eaten directly at every meal of every day in the year, as *tortillas*, *tamales*, and a variety of lesser-known foods such as *atole*, *pinole*, *posole*, etc.

It is worth noting that one of these Peruvian recipes begins by parching the kernel, another by prolonged soaking. The parching (or popping) of the kernel (usually followed by grinding it into a fine meal) is apparently one of the oldest and most widespread uses of maize. It is almost universal in the New World and is widespread in the mountains of central and southeastern Asia. Though many of the products are delicious, they have tended to disappear under the impact of modern sophistication, ultimately to reappear as the ultra-modern, ultra-sophisticated, standardized, mass-produced, trade-marked cocktail wafers such as "Fritos."

As to the prolonged soaking of the kernel, this idea seems to have its roots deep in western South America. Of a collection of recipes obtained from an old family in Antiochia, Colombia, through the kindness of Srta. Julia Guzmán Naranjo, nearly half began by soaking the kernels from overnight to four or five days or longer. It is noteworthy that recipes involving long soaking are apparently unknown to Mexican cooks or considered too trivial for polite discussion.

SUMMARY

1. The common uses of maize are described for the Sierra of Ancash, a somewhat isolated region of Peru north of Lima, with a conservative, predominantly Indian population.

2. The two commonest maize foods in the Sierra of Ancash are *tocos de maíz* and *cancha*. The former is made from kernels fermented under water for two months or longer. The latter consists of whole kernels parched in a special dome-shaped vessel called a *tiesto* or *olla canchera*. Prehistoric examples of these utensils are known from the southern highlands of Peru.

3. These foods are discussed briefly in relation to the history and geographic distribution of uses of maize.

LITERATURE CITED

Biggar, H. P. (1929). The works of Samuel de Champlain. 6 vols. Champlain Soc. Toronto.

Bingham, H. (1930). Machu Picchu, a citadel of the Incas. New Haven.

———, (1948). Lost City of the Incas. 263 pp. New York.

Collins, G. N. (1909). A new type of Indian corn from China. U. S. Dept. Agr. Bur. Plant Ind. Bull. 161:1–30

Cutler, H. C., and Cárdenas, M. (1947). Chicha, a native South American beer. Bot. Mus. Leafl. Harvard Univ. **13**:33–60.

Sprague, G. F., and Jenkins, M. T. (1948). The development of waxy corn for industrial use. Iowa State Coll. Jour. Sci. **22**:205–213.

Weberbauer, A. (1945). El mundo vegetal de los andes peruanos. Min. de Agr. (Lima).

Valcárcel, L. E. (1934). Los trabajos arquelógicos del Cuzco. II. Sajsawaman rediscubierto. Rev. Mus. Nac. (Lima) **3**:211–234.

SPORES OF THE GENUS SELAGINELLA IN NORTH AMERICA NORTH OF MEXICO

ALICE F. TRYON

In 1901 L. M. Underwood remarked that the old *Selaginella rupestris* was one of several examples in which segregation of species had "successively expanded to the bounds that would cause the botanists of twenty years ago to suffer acute paralysis." Among American workers Underwood had already started this segregation three years earlier. The critical studies of Van Eseltine (1918), Maxon (1918, 1920, 1921), and most recently of Weatherby (1944, 1946) have added further new species. Additional collections and critical study will no doubt bring to light still other new species. Dr. Maxon has noted the need for an examination of the species complexes S. *densa* and S. *Wallacei*.

The spores, particularly the characters of the megaspores, have appeared to be an integral part of recent descriptions of species. Mr. Weatherby has expressed the opinion that when used cautiously the pattern of spore sculpture is useful in species definition. The present study was undertaken to present a survey and an illustrated account of the spores of our native Selaginellas.

The megasporangia are not very generously supplied with spores, each usually containing but four megaspores. Each spore has a hemispherical base and three plane triangular faces. The base or *outer face* is the free surface in the tetrad and the three plane triangular surfaces—collectively, the *commissural face*—are the sides in contact in the tetrad. The commissural face is marked by three prominent *commissural ridges* which are united at the apex and radiate out at nearly equal angles to the vicinity of the *equator*. The ends of the ridges are sometimes connected by an *equatorial ring*.

The spore surface may be smooth, granular, rugose, rugose-reticulate, or tuberculate wholly or in part. The enclosed areas in a reticulate pattern are called *areolae*. The photographs convey the type of sculpture more accurately than a descriptive statement, and, unless remarks on variations accompany the data for each species, the illustrations can be regarded as representative of the material examined.

It rarely happens that one or two of the megaspores within a sporangium may develop at the expense of the others, which are then much dwarfed. The megasporangium of S. *rupestris* usually bears two spores although occasionally three or a single spore may develop. The spores of this species characteristically lack commissural ridges but some spores bear a single straight or circular ridge. Occasionally sporangia contain one or two peculiar "dumb-bell"-shaped spores in which there has been an incomplete division (Lyon, 1905). One megasporangium of S. *pilifera* was observed to have eight megaspores.

The size of the megaspores range from 0.15 mm. in diameter in S. *armata* to 0.53 mm. in S. *selaginoides*. The measurements given in the text are of the

greatest diameter. The mode is used to express the central position of the measurements. It is printed in italic between the extremes.

The color of the spores was determined at 45 diameters, using natural light and a black background. The color range is expressed according to Ridgway's 'Color Standards.' The popular term of color approximately equivalent to that of Ridgway's is in parentheses. There is marked variation in color in some species, immature spores often being of a different shade than the mature spores.

The megasporangium was removed from the strobilus and soaked in 50 per cent alcohol. After two or three minutes it was sufficiently pliable to dissect out the spores. Some care had to be used to prevent them from escaping for they were easily blown or jarred from the dissecting field after the alcohol dried. The spores were mounted dry, on a glass or mica slide, within a ring of cement built up to support the cover glass, and this was sealed with cement.

The megaspores were photographed through a compound microscope using a 48-mm. microteliplat lens as the objective and a 15 × hyperplane lens as an ocular. Additional magnification was achieved through suspending a 10 × ocular above the microscope. The camera, a Bausch & Lomb Model K, with 8-inch bellows, was placed over this. An image in focus at the third lens was also in focus on the ground glass of the camera. Four Leitz microscope lamps with green filters were placed around the microscope at the level of the stage. These supplied a very satisfactory source of illumination, for the intensity and angle of the light could be adjusted for each lamp. The film used was Eastman Ortho-X, and the exposure time varied from 20 to 90 seconds.

Each microsporangium bears several hundred microspores which are borne in tetrads and have the same shape as the megaspores and are sculptured in essentially the same manner. The commissural face usually is marked with three commissural ridges although some have a single ridge. The spores of some species have a prominent wing at the equator. The surface of the microspores also bears distinctive markings such as spines, tubercules, or rugae, but it is difficult to find and to recognize mature material. Photographs of the microspores are included when they are representative and show good detail for the species. Twelve spores were measured for each species. The microspores of S. *rupestris* are similar to the megaspores in that they frequently lack the commissural ridges and an occasional dumbbell type is found.

The microspores are roughly about one-eighth as large as the megaspores, ranging from 23 μ in diameter in several species to 64 μ in S. *tortipila*. There is no definite correlation between the size of mega- and microspores of the same species. For example, S. *armata* and S. *selaginoides* have microspores of a similar size while the mode of the megaspores of the former is 0.19 mm. and that of the latter is 0.53 mm. A magnification of at least 400 diameters is necessary to study the surface detail of the microspores, and 70 or 80 diameters is desirable for examination of surface detail of the megaspores.

The microspores are generally more deeply colored than the megaspores, tending toward deep orange or red rather than the lighter yellows, although in some species, as S. *selaginoides*, both mega- and microspores are of the same color.

Slides were prepared by breaking open a microsporangium on a glass slide, adding a drop of lactic acid, and sealing the mount with ringing cement. A lactic acid preparation was more satisfactory than a dry mount, for sculpture not otherwise evident could be distinguished. H. W. Morris, photographer for the University of Minnesota Hospital, photographed the microspores. A homal 3-ocular and a 8-mm. objective were used with a 46-cm. bellows extension of the camera. Illumination was from a carbon arc lamp with a Kaisering green filter. Polychrome plates were used.

The collections studied, for the most part, were identified by such authorities on the genus as Maxon, Van Eseltine, Weatherby, and Wherry. Specimens were examined from the collections of the American Fern Society, Chicago Natural History Museum, Gray Herbarium, University of Minnesota, Missouri Botanical Garden, United States National Museum, and the University of Wisconsin. I wish to express my appreciation to the curators of the herbaria of these institutions who have so kindly lent material for study.

This study has been mainly done at the Missouri Botanical Garden where facilities were generously granted by the Director. The photography was done at the University of Minnesota and the costs incurred supported by the Department of Botany. The problem was initiated at the University of Wisconsin, where a study of *Selaginella* spores was presented as a master's dissertation. I am especially grateful to my husband for the preparation of the photographic unit for the megaspores and for the suggestions and aid given in the study.

Synopsis of Selaginella in North America North of Mexico

The following synopsis has been primarily adapted from the current literature, and references are given to the papers upon which it is based. Since there may be some question regarding the disposition of certain species, now generally reduced to synonymy, it was thought desirable to include photographs and discussion of the spores of these. Characters presented in the synopsis allow it to be used to a certain extent as a key. However, the characters are general ones relating to whole groups and are not necessarily without exception. Each species bears the same number in the text and plates as it does in the synopsis.

SUBGENUS EUSELAGINELLA[1]

Vegetative leaves uniform; sporophylls uniform.

Group of S. selaginoides. Strobilus cylindric..... 1. S. selaginoides (L.) Link

Group of S. rupestris. Strobilus tetragonous.

a. Stems typically erect, rooting only at the base.

b. Setae tortuous.

subgroup of s. tortipila..... 2. S. tortipila A. Br.

2. *S. Sherwoodii* Underw. (see Wherry, 1936)

[1] The subgenera, groups and series are taken from Walton and Alston (1938).

b. Setae straight.

SUBGROUP OF S. BIGELOVII. Megaspores rugose on the outer face....
- 3. S. RUPINCOLA Underw.
- 4. S. CORYI Weatherby
- 5. S. BIGELOVII Underw.
- 6. S. NEOMEXICANA Maxon

SUBGROUP OF S. ARENICOLA. Megaspores smooth or very nearly so on the outer face.....
- 7. S. RIDDELLII Van Eselt.
- 8. S. ARENICOLA Underw.
- *8.* S. *funiformis* Van Eselt. (see Clausen, 1946)
- 9. S. ACANTHONOTA Underw.
- *9.* S. *floridana* Maxon (see Clausen, 1946)

a. Stems prostrate, rooting throughout.

c. Stems radially symmetrical.

SUBGROUP OF S. OREGANA. Stems elongate, slender, branches remote. (see Weatherby, 1944).....
- 10. S. OREGANA D. C. Eaton
- 11. S. UNDERWOODII Hieron.
- 12. S. MUTICA D. C. Eaton
- 13. S. CINERASCENS A. A. Eaton

SUBGROUP OF S. RUPESTRIS. Stems short, stout, branches congested..
- 14. S. WATSONI Underw.
- 15. S. STANDLEYI Maxon
- 16. S. LEUCOBRYOIDES Maxon
- 17. S. WALLACEI Hieron.
- 18. S. SIBIRICA (Milde) Hieron.
- 19. S. ASPRELLA Maxon
- 20. S. DENSA Rydb.
- 21. S. RUPESTRIS (L.) Spring
- 22. S. SCOPULORUM Maxon
- 23. S. WRIGHTII Hieron.

c. Stems strongly dorsiventral.

SUBGROUP OF S. HANSENI. Vegetative leaves uniform or nearly so..
- 24. S. SHELDONI Maxon
- 25. S. HANSENI Hieron.

SUBGROUP OF S. PARISHII. Vegetative leaves dimorphous. (see Weatherby, 1943a).....
- 26. S. ARIZONICA Maxon
- 27. S. EREMOPHILA Maxon

SUBGENUS STACHYGYNANDRUM

Vegetative leaves dimorphous, sporophylls uniform.

SERIES DECUMBENTES. Widely creeping, prostrate, stems rooting throughout.....
- 28. S. DOUGLASII (Hook. & Grev.) Spring
- 29. S. ARMATA Baker
- 30. S. APODA (L.) Fern. (*S. ludoviciana* A. Br.)

SERIES CIRCINATAE. Tufted xerophytes, ascendent, rooted only at the base.. 31. S. LEPIDOPHYLLA (Hook. & Grev.) Spring
32. S. PILIFERA A. Br. (*S. Pringlei* Baker—see Morton, 1939, and Weatherby, 1943b)

DESCRIPTION

SUBGENUS EUSELAGINELLA

GROUP OF S. SELAGINOIDES.—

1. S. SELAGINOIDES (L.) Link. Pl. 23, fig. 1.

Megaspores Barium Yellow (yellow, green-tinged); 0.48–*0.52*–0.53 mm. in diameter, 18 spores measured. *Microspores* Barium Yellow (yellow, green-tinged); 26–34 μ in diameter.

GROUP OF S. RUPESTRIS.—

SUBGROUP OF S. TORTIPILA.—

The two members of this group cannot be distinguished on the basis of spores. This would agree with Wherry's (1936) conclusion that S. *Sherwoodii* is merely an ecological form of S. *tortipila*. The megaspores of S. *Sherwoodii* in the collection examined are strongly tuberculate-rugose. Those of S. *tortipila* are of a similar pattern of sculpture and some are less prominently marked.

2. S. TORTIPILA A. Br. Pl. 23, fig. 2.

Megaspores Straw Yellow to Lemon Chrome (lemon-yellow); 0.25–*0.34*–0.41 mm. in diameter, 26 spores measured. Some spores are more prominently rugose on the outer face than in fig. 2b. *Microspores* Pinard Yellow (pale yellow); 41–64 μ in diameter.

2. S. *Sherwoodii* Underw. Pl. 23, fig. *2.*

Megaspores Apricot Yellow (pale orange); 0.32–0.40 mm. in diameter, 9 spores measured. Some spores are less prominently tuberculate-rugose on the outer face than in fig. *2b*. *Microspores* Apricot-Yellow (pale orange); 38–63 μ in diameter.

SUBGROUP OF S. BIGELOVII.—

Megaspores of S. *rupincola* show a marked variation in prominence of sculpturing. Fig. 3b represents an extreme phase with a well-marked equatorial ring. For the most part, the megaspores examined are sculptured to a less degree as illustrated in fig. 3a, but with a more strongly pronounced equatorial ring. Megaspores of S. *Bigelovii* examined are finely rugose and usually bear an equatorial ring. Some megaspores are marked with subechinate, lace-like prominences which can be seen along the margins of the spores illustrated.

Commissural face of megaspores with moderately coarse rugae; outer face rugose to rugose-tuberculate, ridges low and crowded, areolae narrow if present..... 3. S. RUPINCOLA
Commissural face of megaspores with fine rugae; outer face with low, obscure rugae, areolae small, scarcely distinct from the low, rounded ridges.. 5. S. BIGELOVII

3. S. RUPINCOLA Underw. Pl. 24, fig. 3.

Megaspores Apricot Yellow (pale orange); 0.19–*0.29*–0.34 mm. in diameter, 29 spores measured. *Microspores* Deep Chrome (bright orange); 38–64 μ in diameter.

4. S. CORYI Weath. Am. Fern Jour. 36:51–53. 1946.

Spores of this species were not available for photography but two megaspores from the TYPE have been examined. They are rather similar to those of S. *rupincola* except that they lack an equatorial ring. They are about 0.4 mm. in diameter and Apricot Yellow (pale orange). The rugae are prominent on the outer face and there are distinct areoles between the rugae.

5. S. BIGELOVII Underw. Pl. 24, fig. 5.

Megaspores Apricot Yellow (pale orange); 0.25–*0.34*–0.40 mm. in diameter, 49 spores measured. *Microspores* Apricot Yellow (pale orange); 38–49 μ in diameter.

6. S. NEOMEXICANA Maxon.

Megaspores unknown.

SUBGROUP OF S. ARENICOLA.—

The members comprising this group are difficult to distinguish on the basis of the spores. Clausen (1946) has recognized three species and remarked that of these S. *arenicola* and S. *acanthonota* are not wholly separable. The commissural face is more strongly marked than the outer face in all of the species. However, the sculpturing is rather variable and there appears to be no marked character which distinguishes the species except the degree of prominence of the sculpturing.

The megaspores of S. *Riddellii* are more strongly marked on the outer face than those of the other species. In the collections studied the megaspores of S. *acanthonota* are as prominently rugose-reticulate on the commissural face as those of S. *Riddellii*, and phases of sculpture on the megaspores of S. *acanthonota* and S. *arenicola* are indistinguishable.

Megaspores rugose on outer face	7. S. RIDDELLII
Megaspores smooth on outer face.	
Scarcely rugose on the commissural face	8. S. ARENICOLA 8. S. *funiformis*
Rugose to rugose-tuberculate on commisural face	9. S. ACANTHONOTA 9. S. *floridana*

7. S. RIDDELLII Van Eseltine. Pl. 24, fig. 7.

Megaspores Lemon Chrome (lemon yellow); 0.21–*0.32 & 0.38*–0.46 mm. in diameter, 16 spores measured. The outer face is usually more prominently rugose than in fig. 7b. *Microspores* Apricot Yellow (pale orange); 34–53 μ in diameter.

8. S. ARENICOLA Underw. Pl. 24, fig. 8.

Megaspores White to Apricot Yellow (pale orange); 0.25–*0.29*–0.42 mm. in diameter, 35 spores measured. The outer face is smooth or minutely punctate. *Microspores* Apricot Yellow to Deep Chrome (pale to bright orange); 34–47 μ in diameter.

8. S. *funiformis* Van Eseltine. Pl. 25, fig. *8.*

Megaspores Straw Yellow to Pinard Yellow (pale yellow); 0.21–0.34 mm. in diameter, 6 spores measured. The spores examined are similar in pattern of marking to those of S. *arenicola* but are of a deeper yellow. *Microspores* Deep Chrome (bright orange); 30–41 μ in diameter.

9. S. ACANTHONOTA Underw. Pl. 25, fig. 9.

Megaspores White to Lemon Chrome (lemon yellow); 0.29–*0.36*–0.42 mm. in diameter, 28 spores measured. The pattern of sculpture is similar but the degree of prominence varies between that represented in fig. 9a and 9b. *Microspores* Deep Chrome (bright orange); 34–45 μ in diameter.

9. S. *floridana* Maxon. Pl. 25, fig. *9.*

Megaspores White to Lemon Chrome (lemon yellow); 0.19–*0.32*–0.40 mm. in diameter, 36 spores measured. *Microspores* Deep Chrome (bright orange); 32–53 μ in diameter.

SUBGROUP OF S. OREGANA.—

The group of S. *oregana* as treated by Weatherby (1944) includes several Mexican species and is characterized on the basis of habit. The spores of the species treated here are all distinct and do not appear to indicate relationships between the species.

a. Commissural face of megaspore more prominently rugose than outer face, commissural ridges connected by equatorial ring or free.
  b. Commissural face delicately rugose, commissural ridges thin and delicate.
    c. Outer face slightly reticulate, meshes forming small areolae scarcely more distinct than those of the commissural face..... 10. S. OREGANA
    c. Outer face strongly reticulate, meshes forming broad, shallow areolae more distinct than those on the commissural face..... 11. S. UNDERWOODII
  b. Commissural face coarsely and remotely rugose, commissural ridges broad and coarse; outer face lightly rugose to smooth..... 12. S. MUTICA
a. Commissural face of megaspores lightly rugose, less prominently sculptured than outer face, commissural ridges connected by a prominent, thin equatorial ring..... 13. S. CINERASCENS

10. S. OREGANA D. C. Eaton. Pl. 25, fig. 10.

Megaspores Pinard Yellow (pale yellow); 0.27–*0.32*–0.36 mm. in diameter, 25 spores measured. Some spores bear cross ridges connecting the commissural ridges. *Microspores* Pinard Yellow (pale yellow); 41–56 μ in diameter.

11. S. UNDERWOODII Hieron. Pl. 26, fig. 11.

Megaspores Apricot Yellow (pale orange); 0.27–*0.36*–0.42 mm. in diameter, 38 spores measured. *Microspores* Deep Chrome (bright orange); 30–45 μ in diameter.

12. S. MUTICA D. C. Eaton. Pl. 26, fig. 12.

Megaspores Apricot Yellow (pale orange); 0.21–*0.29*–0.42 mm. in diameter, 31 spores measured. Some spores bear an equatorial ring; some are more strongly rugose-reticulate than fig. 12a. *Microspores* Apricot Yellow (pale orange); 30–53 μ in diameter.

13. S. CINERASCENS A. A. Eaton. Pl. 26, fig. 13.

Megaspores Pinard Yellow (pale yellow); 0.32–*0.37*–0.38 mm. in diameter, 16

spores measured. *Microspores* Apricot Yellow (pale orange); 38–53 μ in diameter.

SUBGROUP OF S. RUPESTRIS.—

The subgroup of S. *rupestris* includes the largest number and the most perplexing species of the subgenus. Several of the species are undoubtedly aggregate groups which need to be extensively collected and critically examined. Maxon (1920, 1921) has investigated some of these and has remarked on relationships between them, but for the most part a natural series has not been worked out.

There is a remarkable similarity between the pattern of sculpture of the megaspores of some of the species. The megaspores of S. *asprella* and one phase of the megaspores of S. *densa* cannot be distinguished. However, there is much variation in the spore sculpture between collections of S. *densa*. Some collections of S. *Watsoni* have megaspores scarcely rugose and very similar in pattern to those of S. *Standleyi;* others have prominently marked spores rather like those of S. *scopulorum*. The megaspores of S. *Wallacei* are variously sculptured but frequently characterized by an equatorial ring.

a. Megaspores 4 per sporangium; 3 commissural ridges.
  b. Outer face obscurely rugose-reticulate to nearly smooth.
    c. Commissural face finely rugose-reticulate..... 14. S. WATSONI
       15. S. STANDLEYI
    c. Commissural face with coarse, low rugae..... 16. S. LEUCOBRYOIDES
  b. Both faces strongly rugose to rugose-tuberculate.
    d. Commissural face with coarse, remote rugae; outer face strongly reticulate, surface of the areolae broad and smooth..... 19. S. ASPRELLA
       20. S. DENSA
    d. Commissural face with delicate, compact rugae; outer face with areolae small or scarcely apparent.
      e. Commissural face strongly rugose to rugose-reticulate; nearly all rugae on outer face joined in a net forming areolae of moderate size.
        f. Equatorial ring usually present..... 17. S. WALLACEI
        f. Without equatorial ring..... 14. S. WATSONI
           18. S. SIBIRICA
           22. S. SCOPULORUM
      e. Both faces with prominent flexuose rugae which have free ends, areolae narrow if present..... 23. S. WRIGHTII
a. Megaspores 2 per sporangium; commissural ridges lacking or a single ridge present..... 21. S. RUPESTRIS

14. S. WATSONI Underw. Pl. 26, fig. 14.

Megaspores Apricot Yellow (pale orange); 0.27–*0.40*–0.50 mm. in diameter, 75 spores measured. The commissural ridges are usually straight and the commissural face somewhat less prominently sculptured than fig. 14a. *Microspores* Deep Chrome (bright orange); 30–53 μ in diameter.

15. S. STANDLEYI Maxon. Pl. 27, fig. 15.

Megaspores Apricot Yellow (pale orange); 0.34–*0.40*–0.48 mm. in diameter, 24 spores measured. Some spores are more prominently rugose than fig. 15. *Microspores* Apricot Yellow (pale orange); 26–41 μ in diameter.

16. S. LEUCOBRYOIDES Maxon Pl. 27, fig. 16.

Megaspores Apricot Yellow (pale orange); 0.32–0.47 mm. in diameter, 8 spores measured. *Microspores* Flame Scarlet (red orange); 38–56 μ in diameter.

17. S. WALLACEI Hieron. Pl. 27, fig. 17.

Megaspores Apricot Yellow (pale orange); 0.27–*0.34*–0.38 mm. in diameter, 51 spores measured. Some spores are less prominently sculptured than fig. 17, and some are without an equatorial ring. *Microspores* Deep Chrome (bright orange); 38–49 μ in diameter.

18. S. SIBIRICA (Milde) Hieron. Pl. 27, fig. 18.

Megaspores Pinard Yellow to Apricot Yellow (pale yellow to pale orange); 0.38–*0.40*–0.42 mm. in diameter, 5 spores measured. The commissural ridges are usually twice as long as those in fig. 18a. *Microspores* Deep Chrome (bright orange); 38–49 μ in diameter.

19. S. ASPRELLA Maxon. Pl. 28, fig. 19.

Megaspores Straw Yellow to Apricot Yellow (pale orange); 0.29–*0.34*–0.38 mm. in diameter, 6 spores measured. Some spores have an equatorial ring. *Microspores* Pinard Yellow to Deep Chrome (bright yellow to bright orange); 34–53 μ in diameter.

20. S. DENSA Rydb. Pl. 28, fig. 20.

Megaspores Apricot Yellow (pale orange); 0.36–*0.40*–0.50 mm. in diameter, 48 spores measured. The spores photographed are from type material and illustrate the pattern of sculpture in several of the collections studied. *Microspores* Deep Chrome (bright orange); 34–49 μ in diameter.

21. S. RUPESTRIS (L.) Spring. Pl. 28, fig. 21.

Megaspores Deep Chrome (bright orange); 0.32–*0.46*–0.53 mm. in diameter, 53 spores measured. The sculpture of the spores examined is generally of the same pattern, varying in the prominence of reticulation. *Microspores* Apricot Yellow (pale orange); spores monolete, 49–75 μ in greatest dimension.

22. S. SCOPULORUM Maxon. Pl. 28, fig. 22.

Megaspores Deep Chrome (bright orange); 0.32–*0.42*–0.48 mm. in diameter, 35 spores measured. *Microspores* Apricot Yellow (pale orange); 34–56 μ in diameter.

23. S. WRIGHTII Hieron. Pl. 29, fig. 23.

Megaspores Apricot Yellow to Deep Chrome (pale to bright orange); 0.18–*0.25*–0.55 mm. in diameter, 44 spores measured. There is considerable variation in size of spores of this species, since one large spore may develop at the expense of three small spores within a megasporangium. The pattern of sculpture of the spores is generally similar. *Microspores* Deep Chrome (bright orange); 34–56 μ in diameter.

SUBGROUP OF S. HANSENI.—

The two species of this subgroup are allied on the basis of strongly dorsiventral stems and uniform leaves. The spores are distinctive for each species.

Commissural face of megaspores without equatorial ring; strongly reticulate on outer face ..... 24. S. SHELDONI
Commissural face of megaspores with prominent equatorial ring; lightly rugose on outer face ..... 25. S. HANSENI

24. S. Sheldoni Maxon. Pl. 29, fig. 24.

Megaspores Deep Chrome (bright orange); 0.34–*0.36*–0.44 mm. in diameter, 28 spores measured. *Microspores* Deep Chrome (bright orange); 34–45 μ in diameter.

25. S. Hanseni Hieron. Pl. 29, fig. 25.

Megaspores Lemon Chrome (lemon yellow); 0.29–*0.36*–0.42 mm. in diameter, 40 spores measured. *Microspores* Apricot Yellow (pale orange); 38–49 μ in diameter.

SUBGROUP OF S. PARISHII.—

Two members of this group are Mexican and are not treated here. The megaspores of S. *eremophila* are for the most part more prominently sculptured than the megaspores of S. *arizonica*. In both species a single, large megaspore and three small spores may be found within a sporangium.

Commissural face of megaspore finely rugose-reticulate; scarcely marked with equatorial ring; outer face coarsely reticulate to smooth ..... 26. S. arizonica
Commissural face of megaspore with sharp, projecting rugae, prominent equatorial ring; outer face deeply rugose-reticulate ..... 27. S. eremophila

26. S. arizonica Maxon. Pl. 29, fig. 26.

Megaspores Apricot Yellow (pale orange); 0.25–*0.32*–0.46 mm. in diameter, 36 spores measured. Some spores are more prominently marked than fig. 26b; some have an obscure equatorial ring. *Microspores* Deep Chrome (bright orange); 23–38 μ in diameter.

27. S. eremophila Maxon. Pl. 29, fig. 27.

Megaspores Pinard Yellow (pale yellow); 0.23–*0.34*–0.50 mm. in diameter, 25 spores measured. *Microspores* Deep Chrome (bright orange); 38–53 μ in diameter.

SUBGENUS STACHYGYNANDRUM

The species included in this study belonging to this subgenus are all characterized by strikingly distinct spores. The microspores are as strongly marked as the megaspores. The microspores of S. *apoda* and S. *Douglasii* have a pebbled appearance, those of S. *armata* are beset with papillae and those of S. *pilifera* have globules of a waxy substance adhering to them.

Series Decumbentes.—

Megaspores less than 0.22 mm. in diameter; deep yellow to orange; obscurely rugose to nearly smooth ..... 29. S. armata
Megaspores more than 0.36 mm. in diameter; straw-yellow or lighter with a green-tinge; strongly marked.
  Megaspores granular to tuberculate ..... 28. S. Douglasii
  Megaspores marked with prominent, thin, free rugae ..... 30. S. apoda

28. S. Douglasii (Hook. & Grev.) Spring. Pl. 30, fig. 28.

Megaspores Straw Yellow; 0.36–*0.38*–0.40 mm. in diameter, 7 spores measured. *Microspores* Deep Chrome (bright orange); 23–41 μ in diameter.

29. S. armata Baker. Pl. 30, fig. 29.

Megaspores Deep Chrome (bright orange); 0.15–*0.19*–0.21 mm. in diameter, 15 spores measured. *Microspores* Flame Scarlet (red orange); 26–34 μ in diameter.

30. S. APODA (L.) Fern. Pl. 30, fig. 30.

Megaspores Barium Yellow (yellow, green-tinged); 0.34–0.36 mm. in diameter, 7 spores measured. *Microspores* Flame Scarlet (red orange); 23–34 μ in diameter.

SERIES CIRCINATAE.—

Megaspores spinulose ..... 31. S. LEPIDOPHYLLA
Megaspores granular ..... 32. S. PILIFERA

31. S. LEPIDOPHYLLA (Hook. & Grev.) Spring. Pl. 30, fig. 31.

Megaspores Deep Chrome (bright orange); 0.23–*0.29*–0.42 mm. in diameter, 23 spores measured. *Microspores* adhere in tetrads which are Flame Scarlet (red orange).

32. S. PILIFERA A. Br. Pl. 30, fig. 32.

Megaspores Straw Yellow to Pinard Yellow (pale orange); 0.25–0.29 mm. in diameter, 11 spores measured. Some spores have an equatorial ring. *Microspores* Flame Scarlet (red orange); 26–38 μ in diameter.

BIBLIOGRAPHY

Baker, J. G. (1887). Handbook of the fern allies. London.

Broun, M. (1938). Index to North American ferns. Orleans, Mass.

Clausen, R. T. (1946). *Selaginella,* subgenus Euselaginella, in the southeastern United States. Am. Fern Jour. **36**:65–82.

Hieronymus, G. (1900). Selaginellarum species novae vel non satis cognitae. I. Hedwigia **39**:290–320.

Lyon, F. M. (1901). A study of the sporangia and gametophytes of *Selaginella apus* and *Selaginella rupestris*. Bot. Gaz. **32**:124–141, 170–194.

———, (1905). The spore coats of *Selaginella*. *Ibid*. **40**:285–295.

Maxon, W. R. (1918). A new *Selaginella* from Oklahoma and Texas. Proc. Biol. Soc. Wash. **31**:171–172.

———, (1920). New Selaginellas from the western United States. Smithson. Misc. Coll. **72**[5]:1–10.

———, (1921). Notes on American ferns—XVII. Am. Fern Jour. **11**:34–39.

———, (1923). Notes on American ferns—XIX. *Ibid*. **13**:73–75.

Morton, C. V. (1939). Our southwestern resurrection plants. *Ibid*. **29**:14–16.

Reeve, R. M. (1935). The spores of the genus *Selaginella* in north central and north eastern United States. Rhodora **37**:341–345.

Ridgway, Robert (1912). Color standards and color nomenclature. Washington, D. C.

Selling, O. H. (1946). Studies in Hawaiian pollen statistics. Pt. I. Bishop Mus. Spec. Publ. 37.

Underwood, L. M. (1898). *Selaginella rupestris* and its allies. Bull. Torrey Bot. Club **25**:125–133.

———, (1901). A changed conception of species. Fern Bull. **9**:49–53.

Van Eseltine, G. P. (1918). The allies of *Selaginella rupestris* in the southeastern United States. Contr. U. S. Nat. Herb. **20**:159–172.

Walton, J., and A. H. G. Alston (1938). Lycopodiinae in Verdoorn, Manual of Pteridology. pp. 503–506.

Weatherby, C. A. (1943a). The group of *Selaginella Parishii*. Am. Fern Jour. **33**:113–119.

———, (1943b). Selaginellaceae, in Johnston, I. M., Plants of northern Mexico, I. Jour. Arn. Arb. **24**:325–329.

———, (1944). The group of *Selaginella oregana* in North America. *Ibid*. **25**:407–419.

———, (1946). A new *Selaginella* from western Texas. Am. Fern Jour. **36**:51–53.

Wherry, E. T. (1936). Observations on *Selaginella tortipila*. Jour. So. Appalach. Bot. Club **1**:65–69.

Explanation of Plate

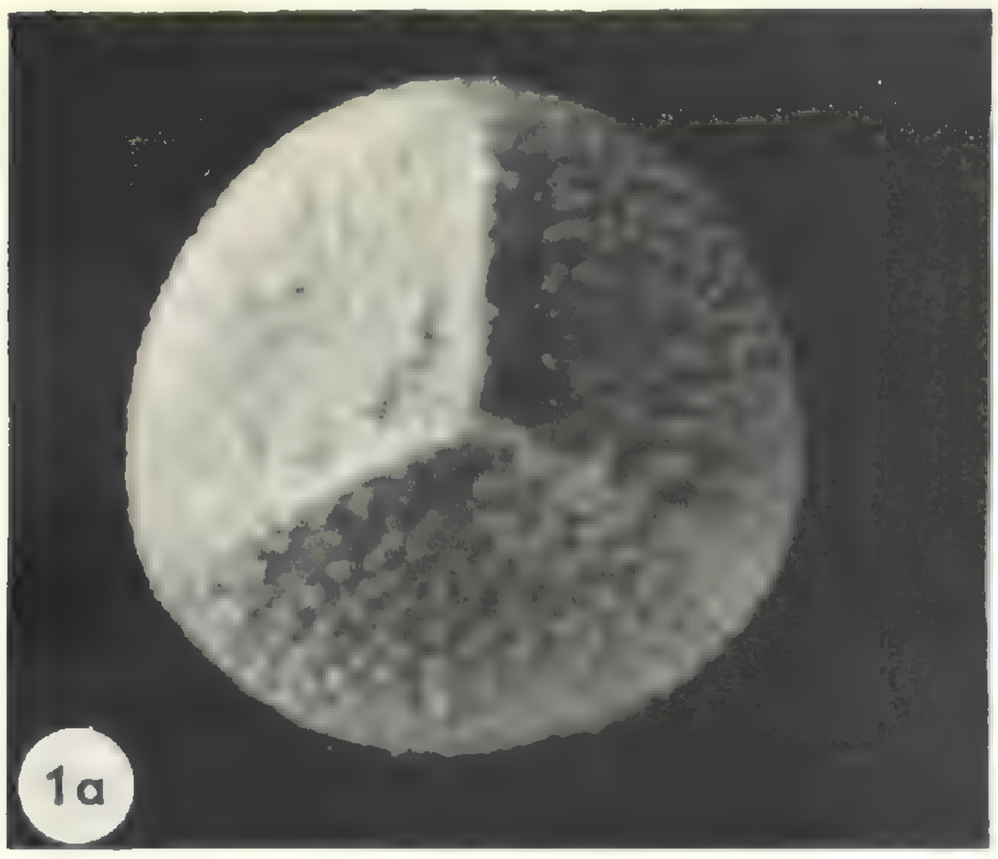
In this and the following plates, which are reproductions of photographs, the magnification for the megaspores is 85 diameters and for the microspores 450 diameters.

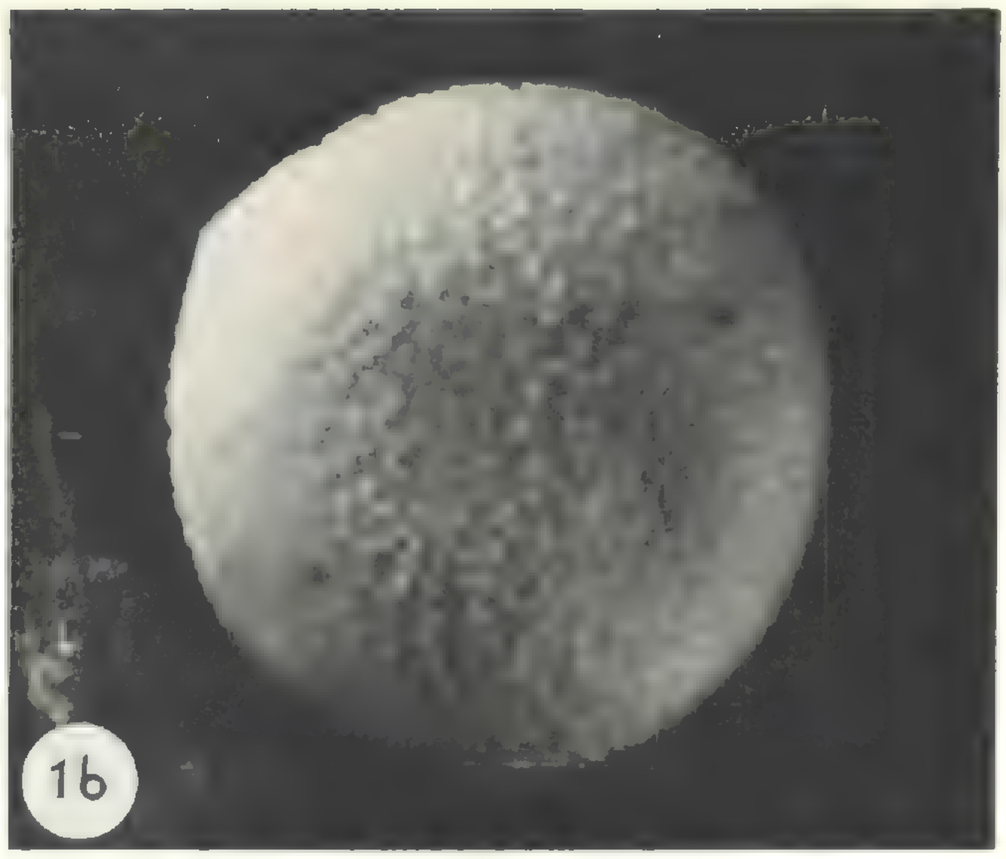
PLATE 23

Fig. 1. S. SELAGINOIDES: *Butters & Holway,* Alberta, 1905 (Univ. Minn.). 1a. Commissural face of megaspore. 1b. Outer face of megaspore.

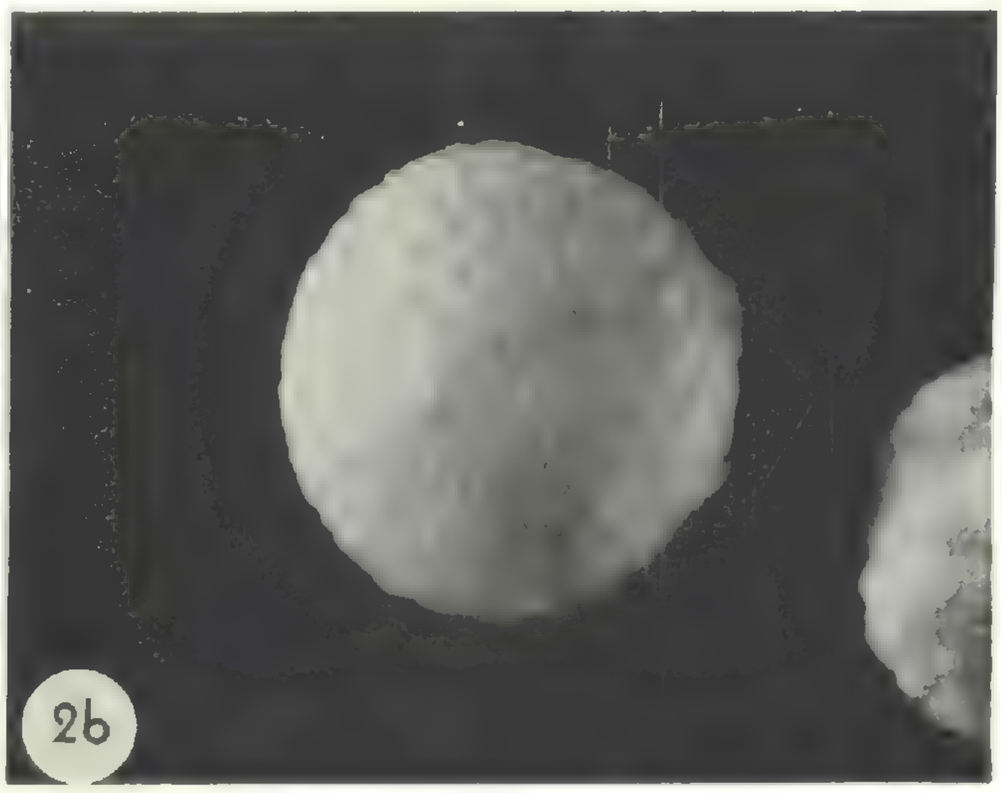
Fig. 2. S. TORTIPILA: *Donnell-Smith,* South Carolina, 1881 (Chicago Nat. Hist. Mus.). 2a. Commissural face of megaspore. 2b. Outer face of a moderately marked spore.

Fig. *2.* S. *Sherwoodii: Donnell-Smith,* North Carolina, 1882 (Mo. Bot. Gard.). *2a.* Commissural face of megaspore. *2b.* Outer face of a strongly marked megaspore. *2c.* Microspore.

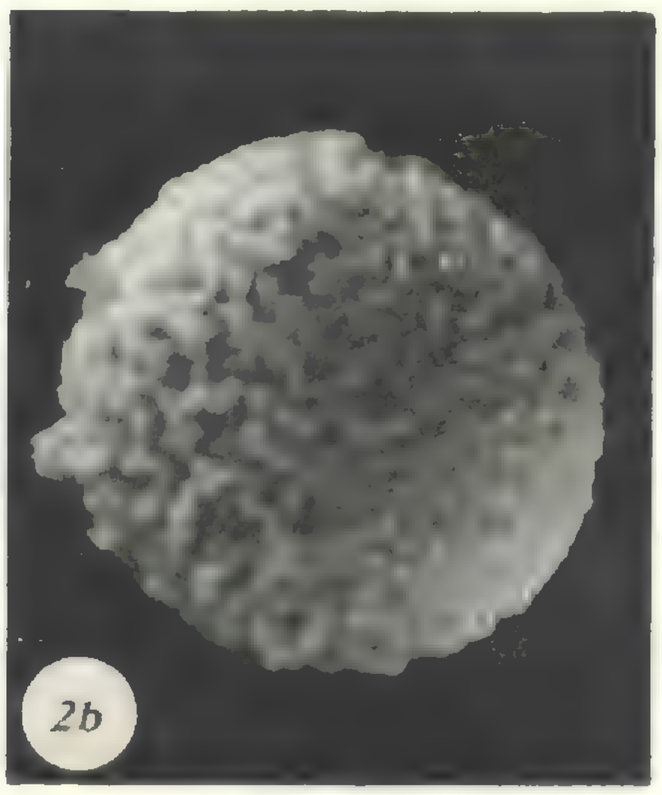




S. SELAGINOIDES

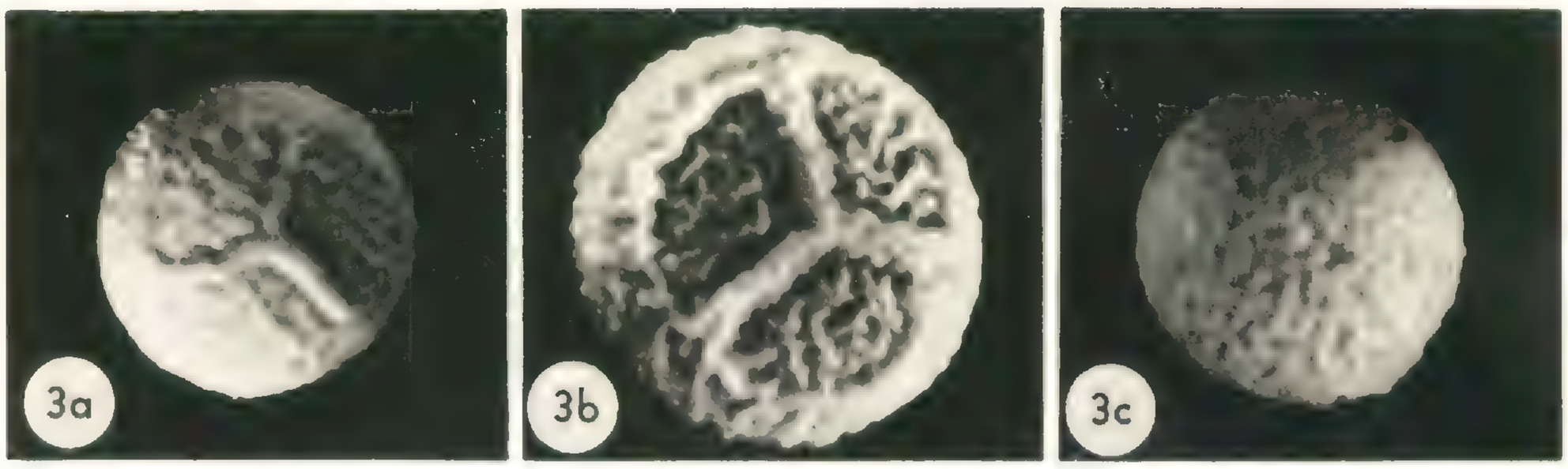


S. TORTIPILA

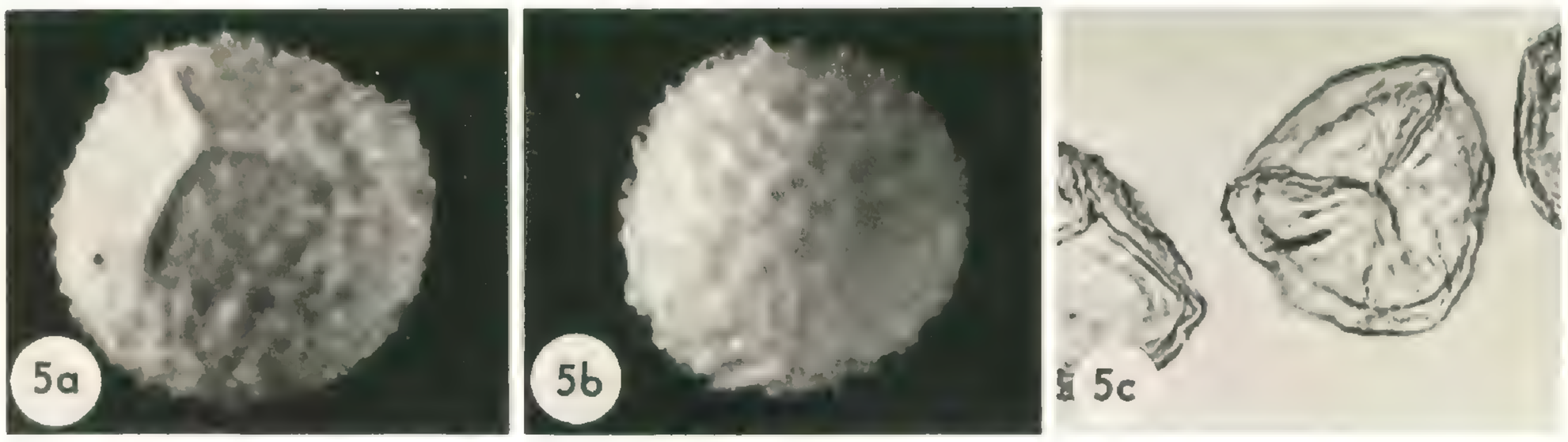


S. Sherwoodii

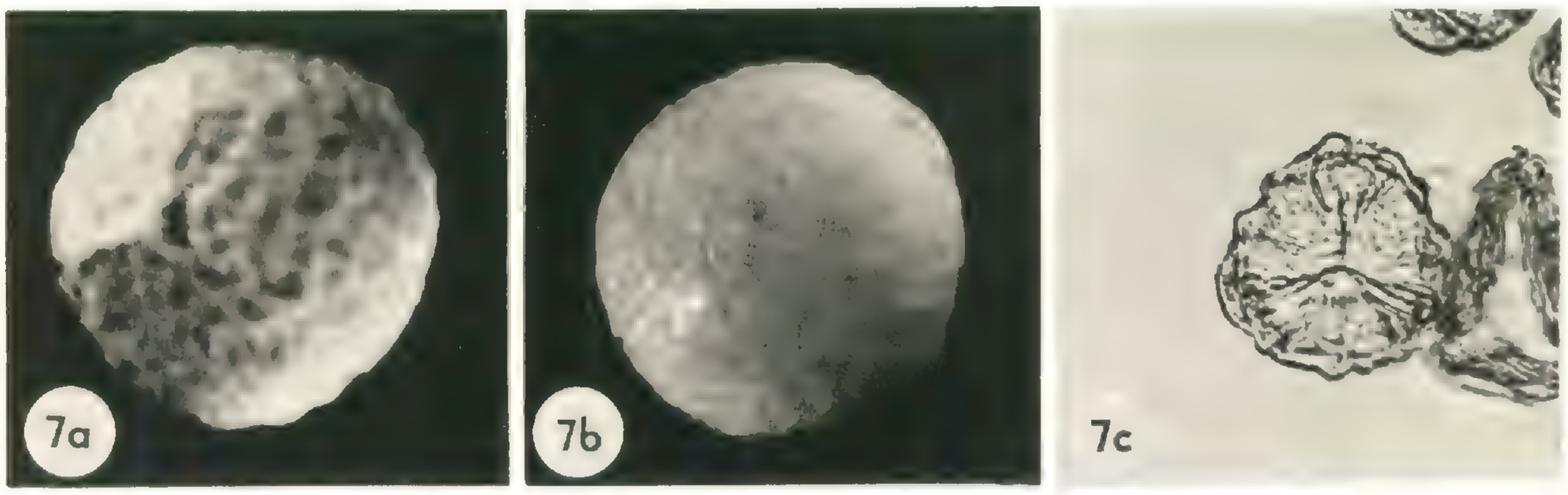
TRYON — SELAGINELLA SPORES



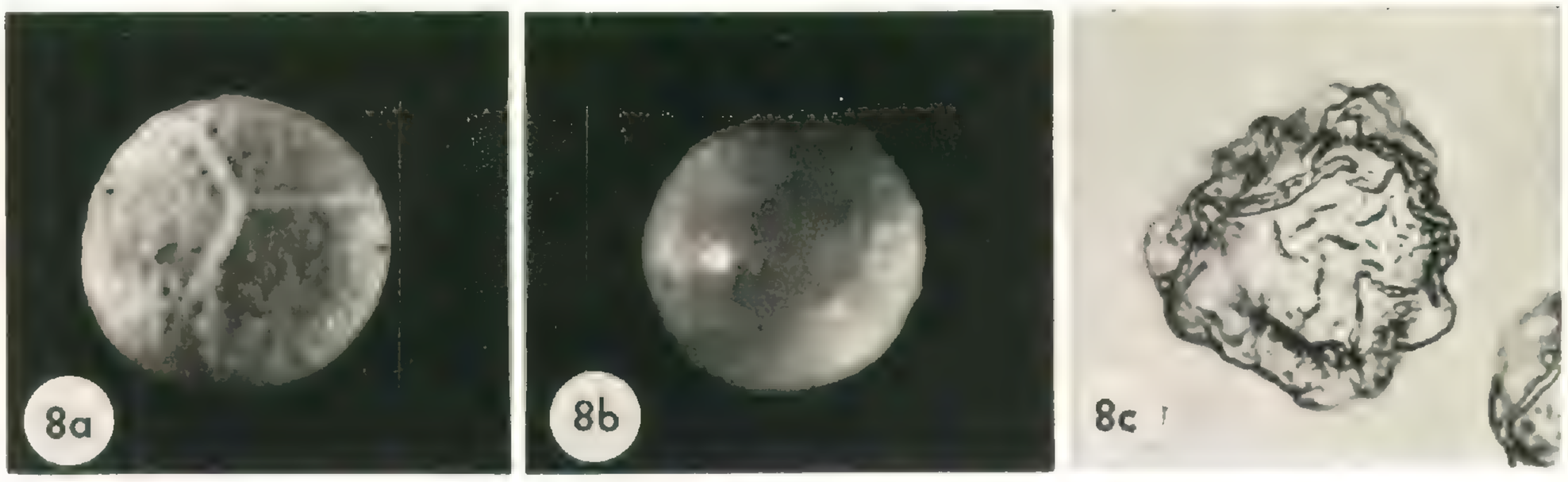
S. RUPINCOLA



S. BIGELOVII



S. RIDDELLII



S. ARENICOLA

Explanation of Plate

PLATE 24

Fig. 3. S. RUPINCOLA: 3a. Commissural face of megaspore, *Goodding*, Arizona, 1921 (Chicago Nat. Hist. Mus.). 3b. Commissural face of prominently sculptured megaspore, *Wooton*, New Mexico, 1907 (Univ. Minn.). 3c. Outer face of megaspore, from the same specimen as 3a.

Fig. 5. S. BIGELOVII: 5a. Commissural face of megaspore without prominent equatorial ring, *Rose 34495*, California, 1932 (Chicago Nat. Hist. Mus.). 5b. Outer face of megaspore, *Grant & Wheeler*, California, 1904 (Univ. Minn.). 5c. Microspore from the same specimen as 5a.

Fig. 7. S. RIDDELLII: *Cory 41099*, Texas, 1943 (Gray Herb.). 7a. Commissural face of megaspore. 7b. Outer face of a lightly marked megaspore. 7c. Microspore.

Fig. 8. S. ARENICOLA: *Deam 63923*, Florida, 1946 (Mo. Bot. Gard.). 8a. Commissural face of megaspore. 8b. Outer face of megaspore. 8c. Microspore.

Explanation of Plate

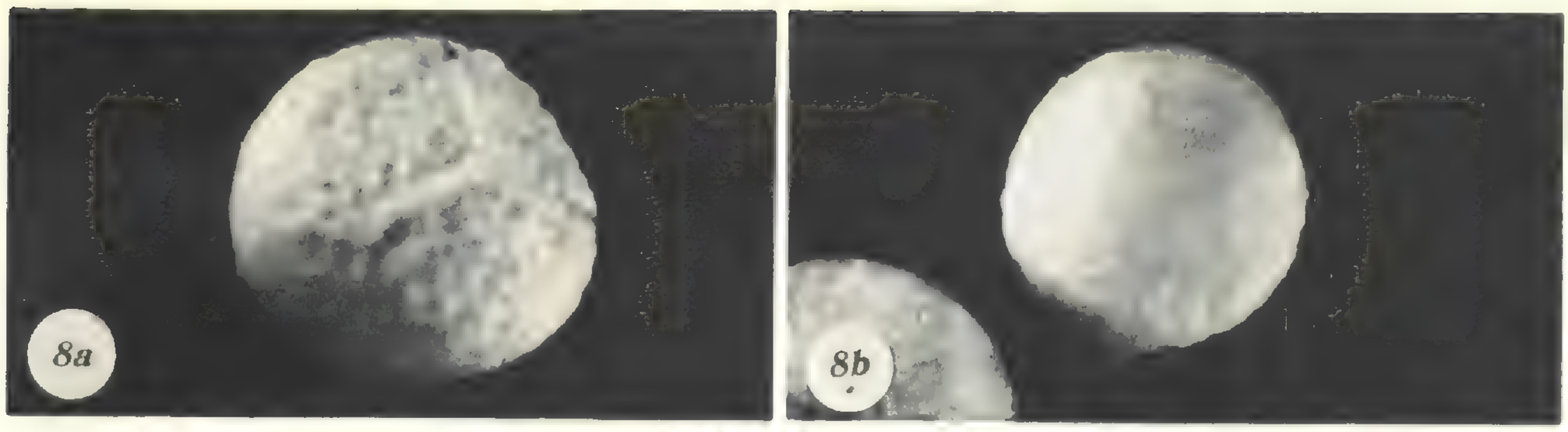
PLATE 25

Fig. 8. S. *funiformis: O'Neill 7580,* Florida, 1933 (Chicago Nat. Hist. Mus.). *8a.* Commissural face of megaspore. *8b.* Outer face of megaspore.

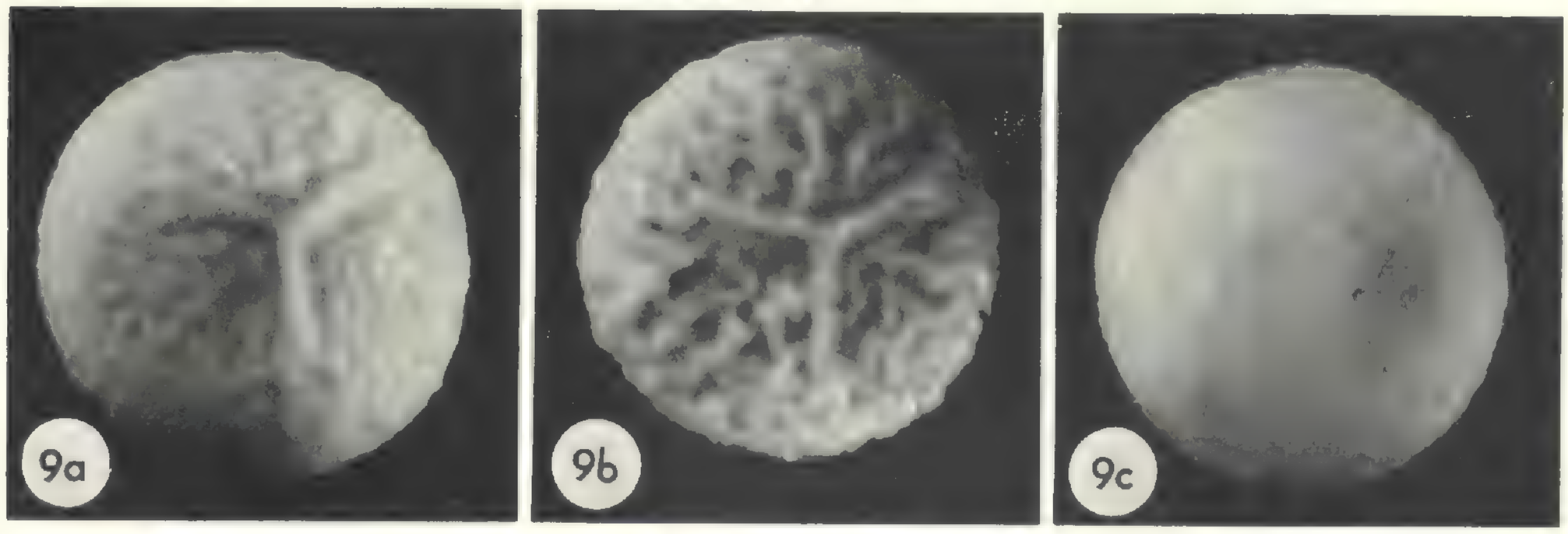
Fig. 9. S. ACANTHONOTA: 9a. Commissural face of a lightly marked megaspore, *Pyron & McVaugh 3101,* Georgia, 1938 (Mo. Bot. Gard.). 9b. Commissural face of a prominently marked megaspore, *Harper 1057,* Georgia, 1903 (Mo. Bot. Gard.). 9c. Outer face of megaspore, from same specimen as 9a.

Fig. 9. S. *floridana: Nash 1449,* Florida, 1894, Isotype (Chicago Nat. Hist. Mus.). *9a.* Commissural face of megaspore. *9b.* Outer face of megaspore.

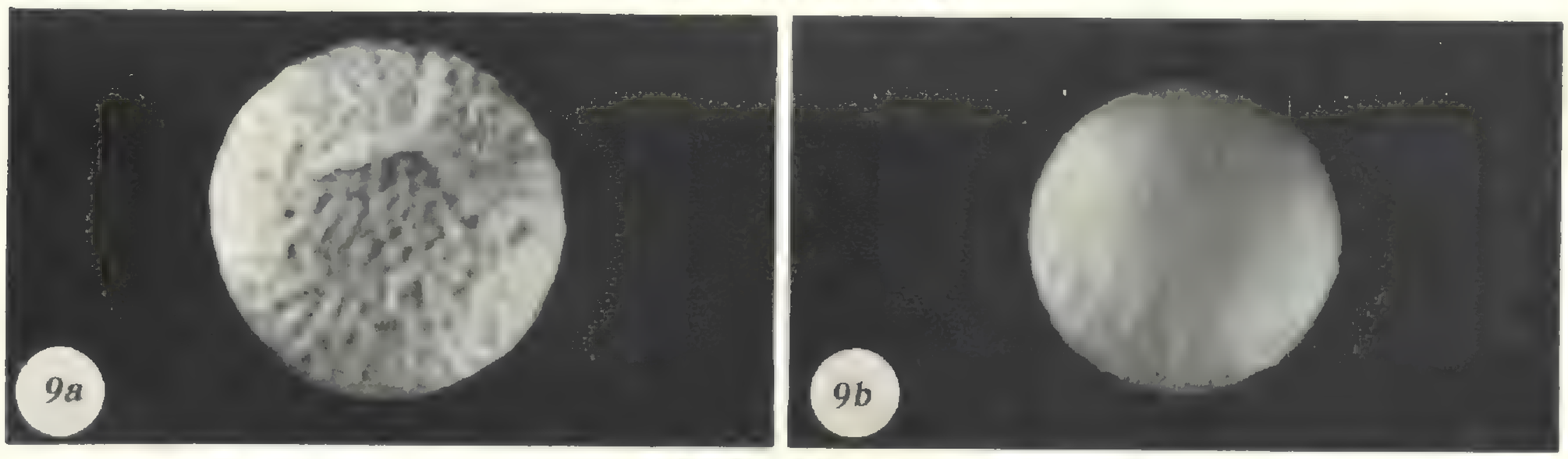
Fig. 10. S. OREGANA: *Piper,* Washington, 1893 (Univ. Minn.). 10a. Commissural face of megaspore. 10b. Outer face of megaspore. 10c. Microspore.



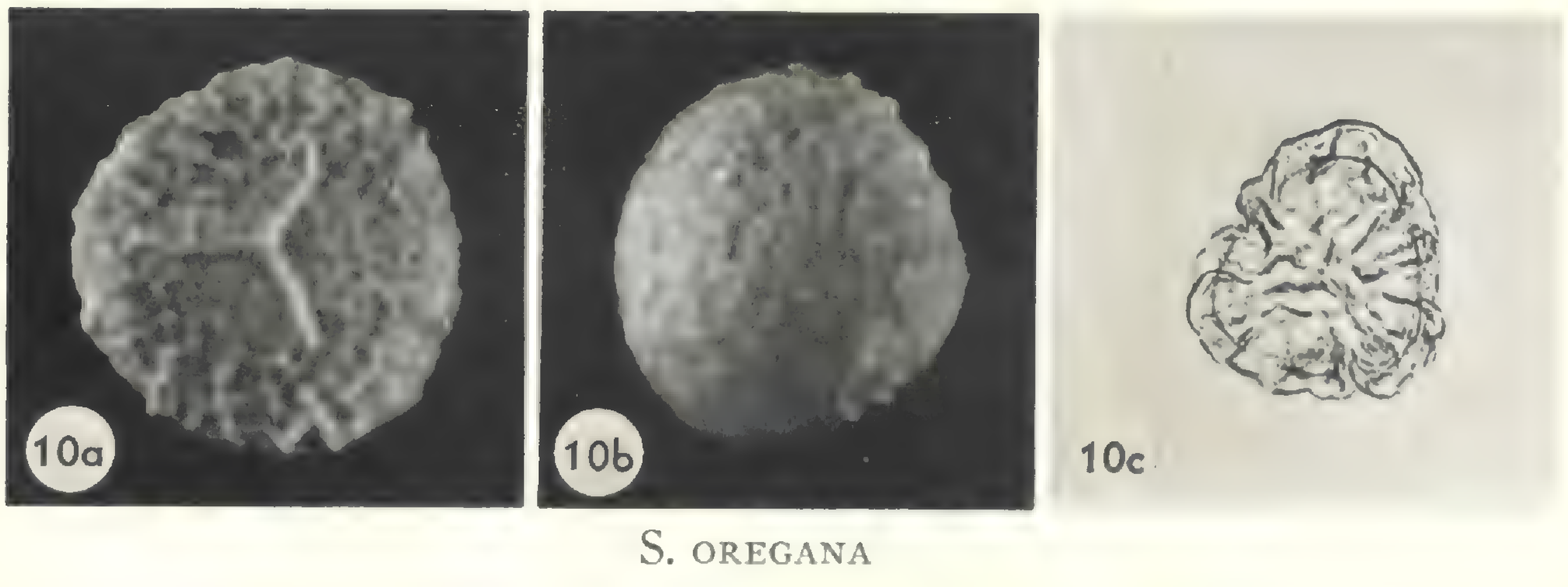
S. funiformis



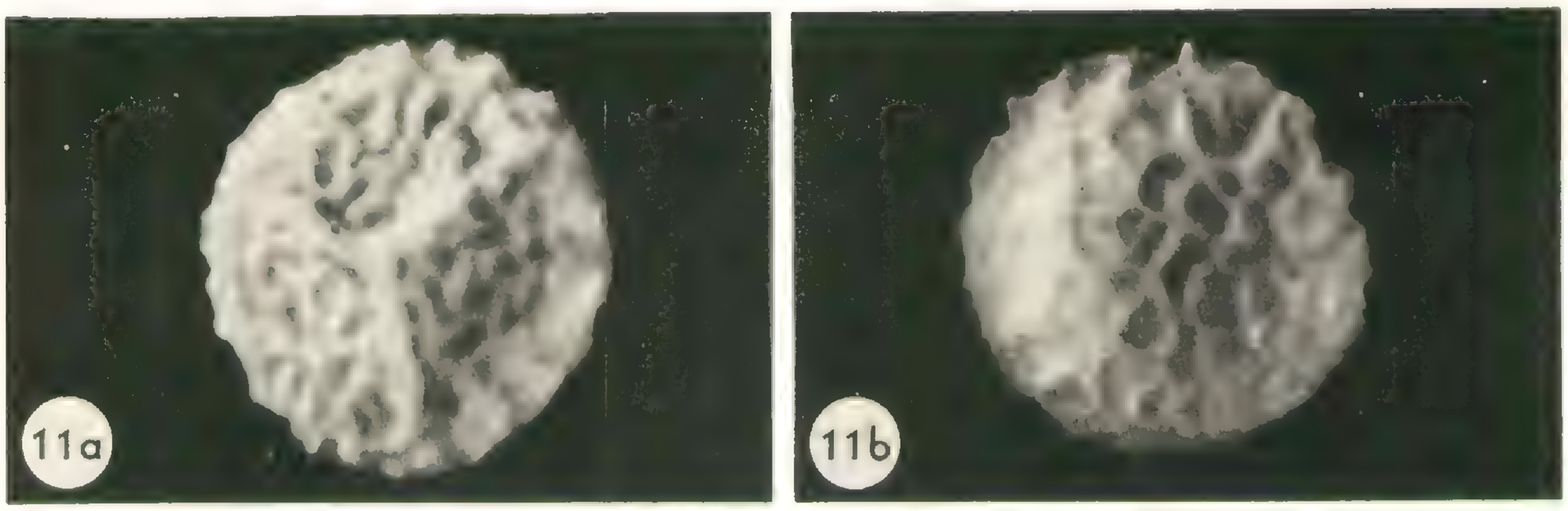
S. ACANTHONOTA



S. floridana



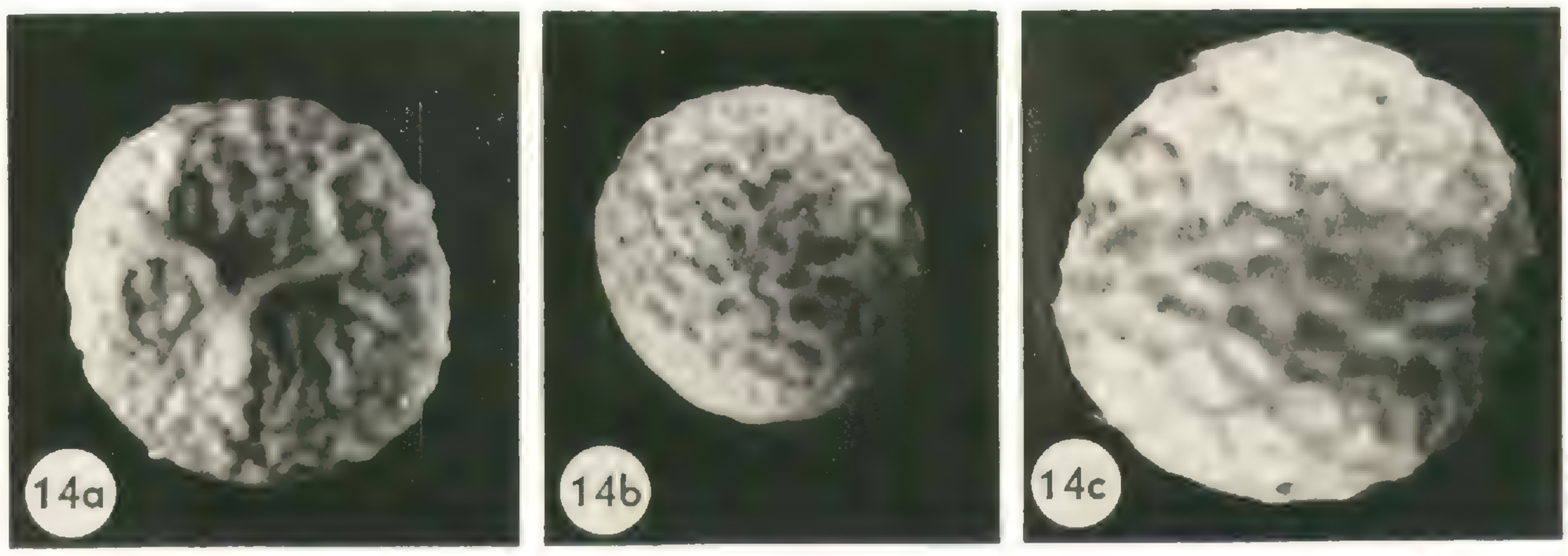
S. OREGANA



S. UNDERWOODII

S. MUTICA

S. CINERASCENS



S. WATSONI

TRYON — SELAGINELLA SPORES

Explanation of Plate

PLATE 26

Fig. 11. S. Underwoodii: 11a. Commissural face of megaspore (var. *dolichotricha* Weath.), *Metcalfe 991*, New Mexico (Mo. Bot. Gard.). 11b. Outer face of megaspore, *Clark 8968*, Arizona, 1940 (Mo. Bot. Gard.).

Fig. 12. S. mutica: *Drouet, Richards & Rubinstein 4097*, Colorado, 1941 (Mo. Bot. Gard.). 12a. Commissural face of a lightly marked spore without an equatorial ring. 12b. Outer face of megaspore. 12c. Microspore.

Fig. 13. S. cinerascens: *Abrams 3399*, California, 1903 (Chicago Nat. Hist. Mus.). 13a. Commissural face of megaspore. 13b. Outer face of megaspore.

Fig. 14. S. Watsoni: *Maguire, Hobson & Maguire 14729*, Utah, 1936 (U. S. Nat. Herb.). 14a. Commissural face of a prominently marked megaspore with unusual flexuose commissural ridges. 14b. Outer face of megaspore. 14c. Outer face of megaspore with large areolae. 14d. Microspore.

Explanation of Plate

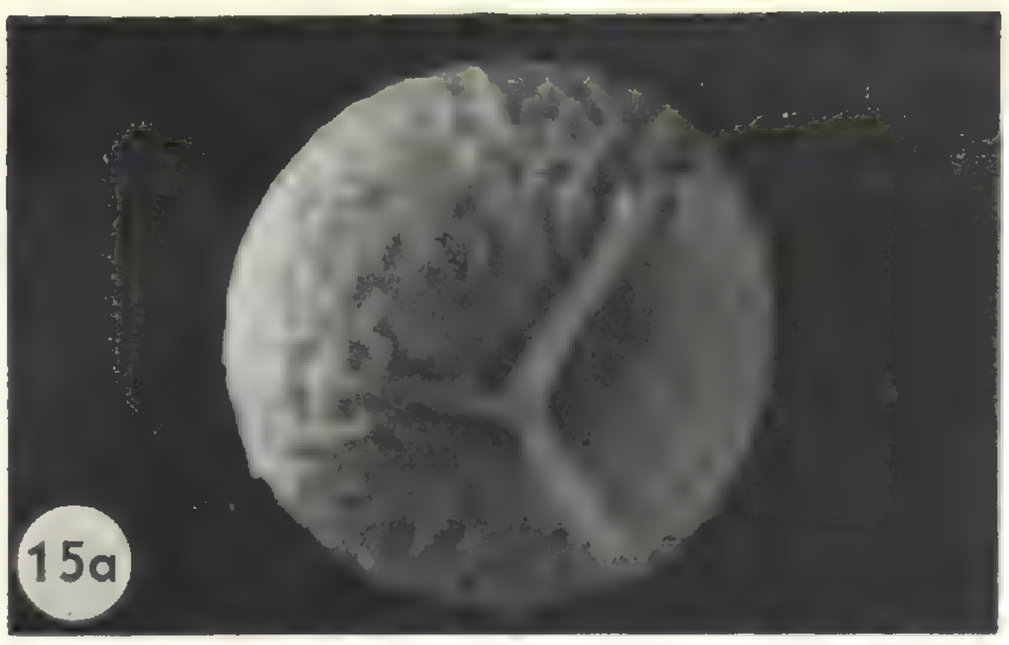
PLATE 27

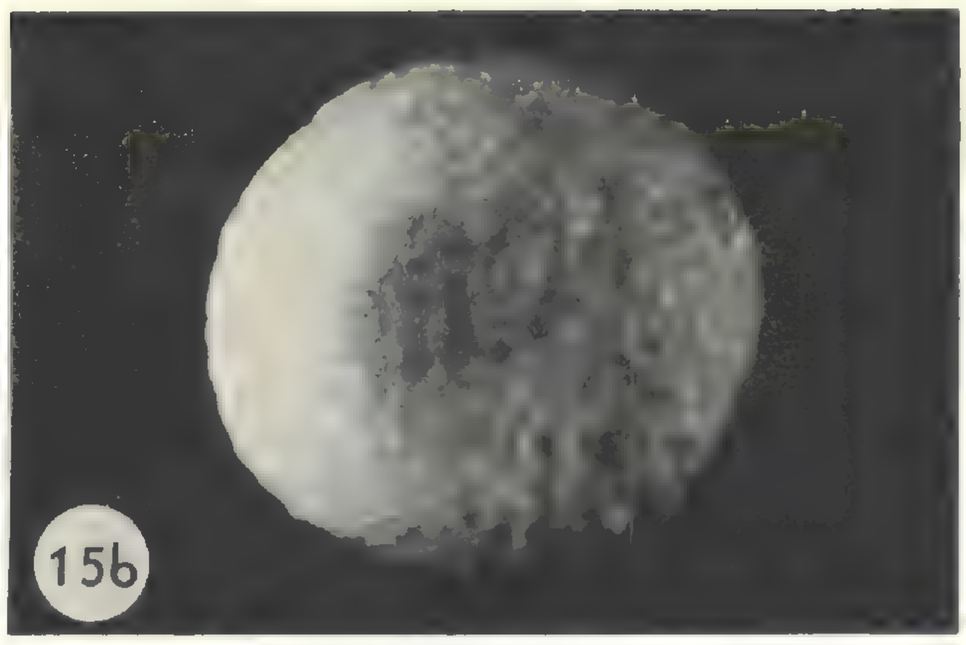
Fig. 15. S. Standleyi: *Wherry,* Colorado (U. S. Nat. Herb. 1730847). 15a. Commissural face of a lightly marked megaspore. 15b. Outer face of a lightly marked megaspore.

Fig. 16. S. leucobryoidis: *Munz & Harwood 3780,* California, 1920, Isotype (Chicago Nat. Hist. Mus.). 16a. Commissural face of a lightly marked megaspore. Note microspore attached near end of one commissural ridge. 16b. Outer face of microspore.

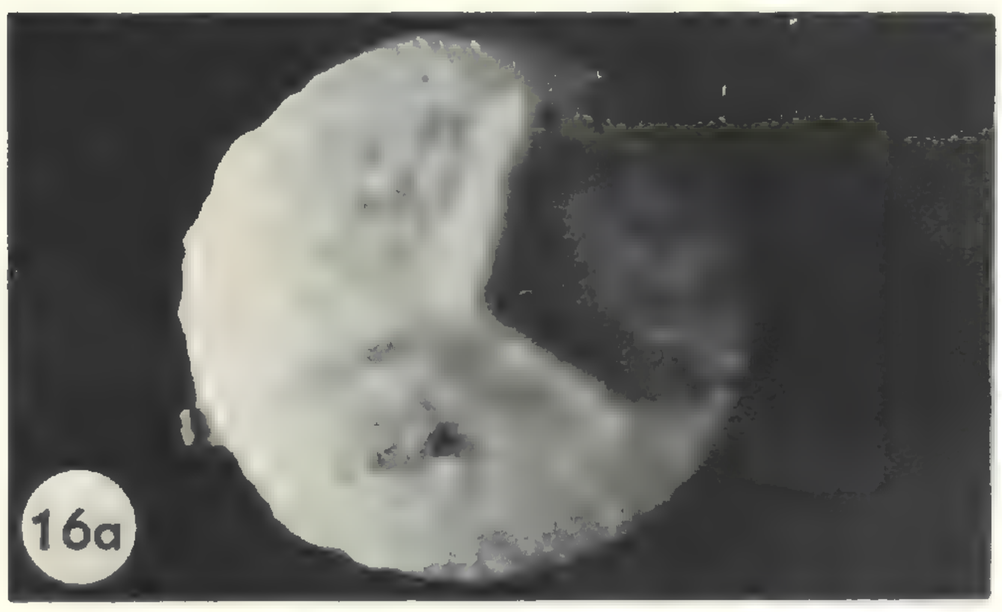
Fig. 17. S. Wallacei: *Constance & Rollins 998,* Washington, 1935 (Univ. Minn.). 17a. Commissural face of a prominently marked megaspore with prominent equatorial ring. 17b. Outer face of a prominently marked megaspore.

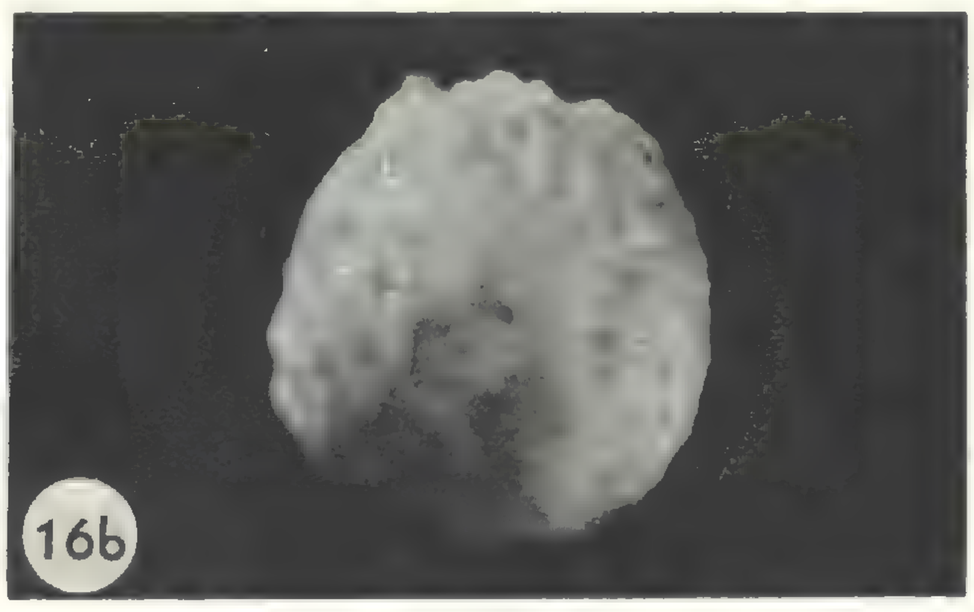
Fig. 18. S. sibirica: *Porsild 150,* Alaska, 1926 (Gray Herb.). 18a. Commissural face of a megaspore with unusually short commissural ridges. 18b. Outer face of megaspore.



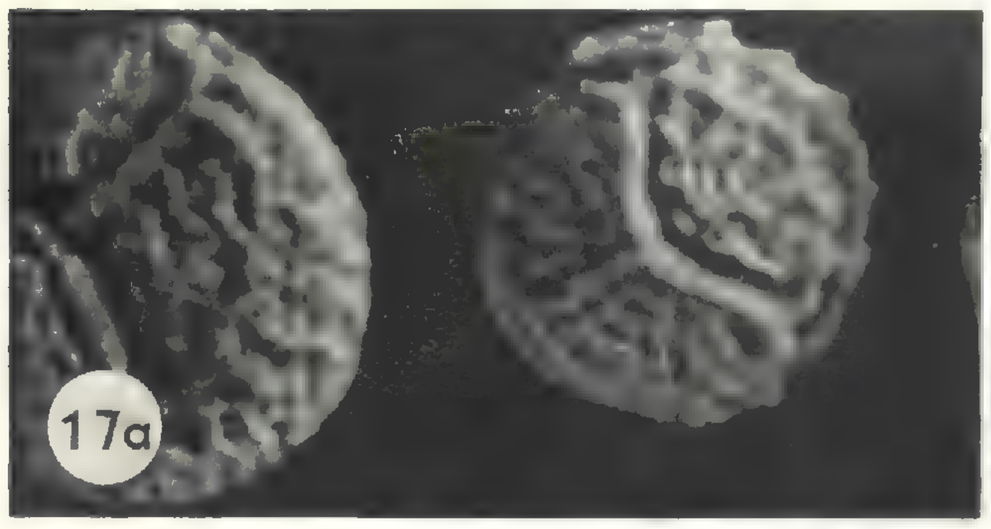


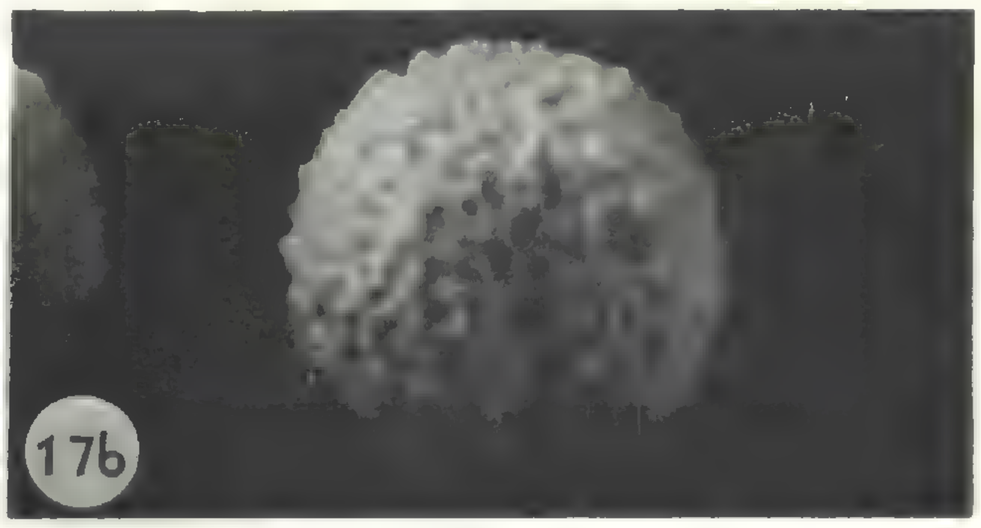
S. STANDLEYI



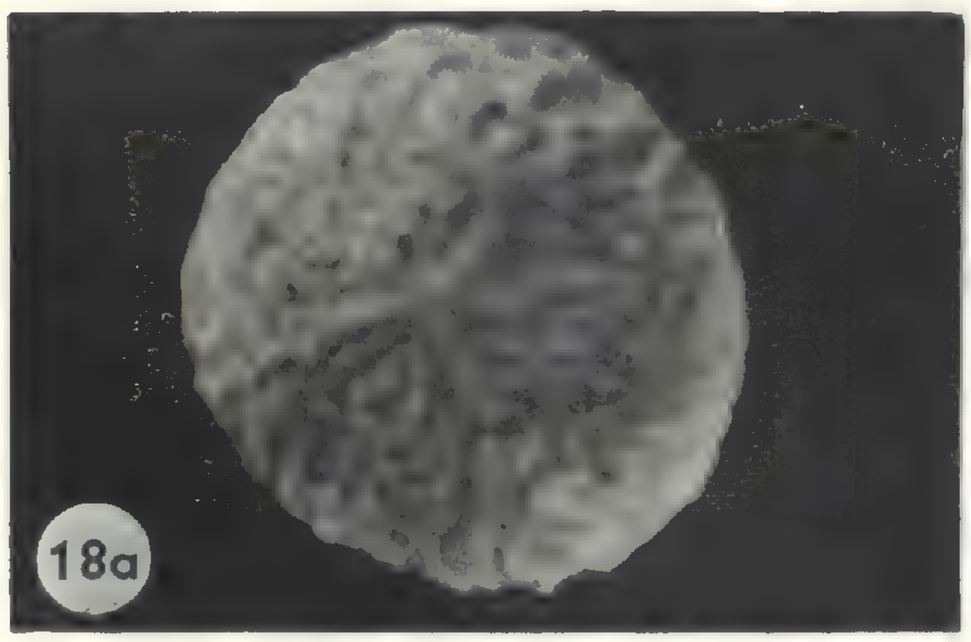


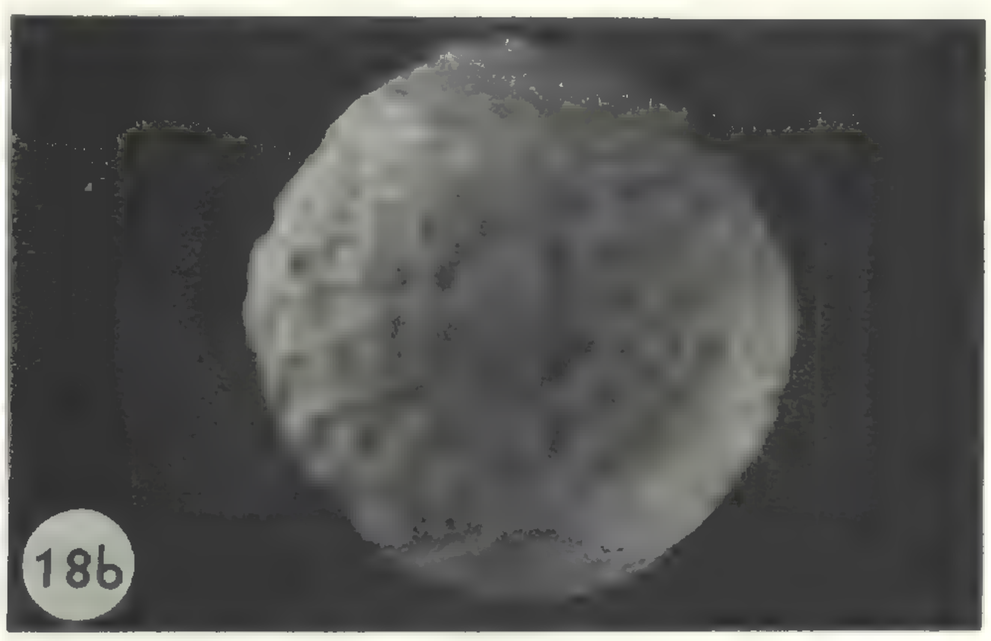
S. LEUCOBRYOIDES





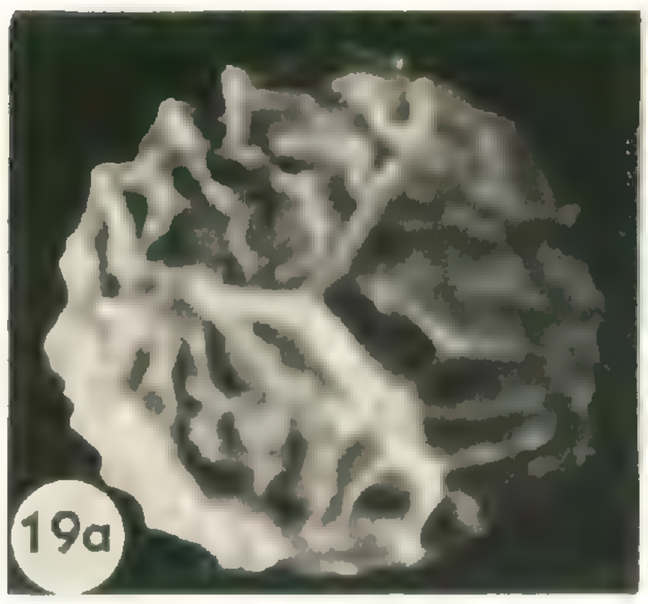
S. WALLACEI

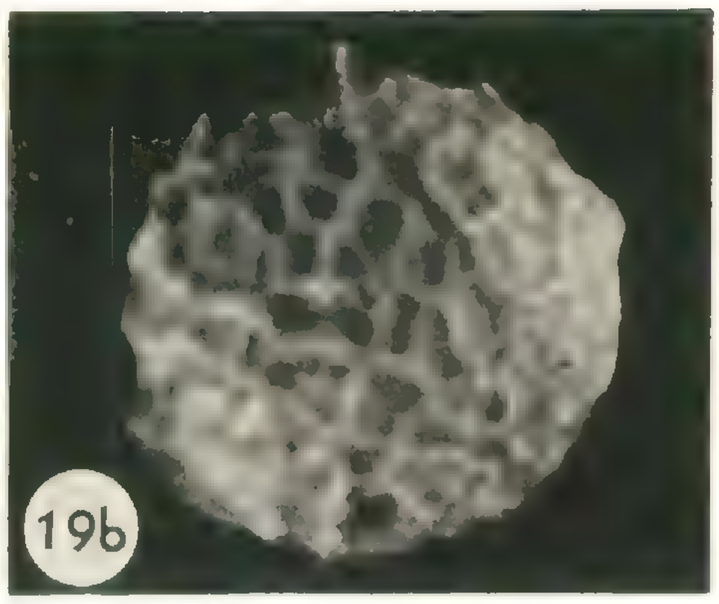


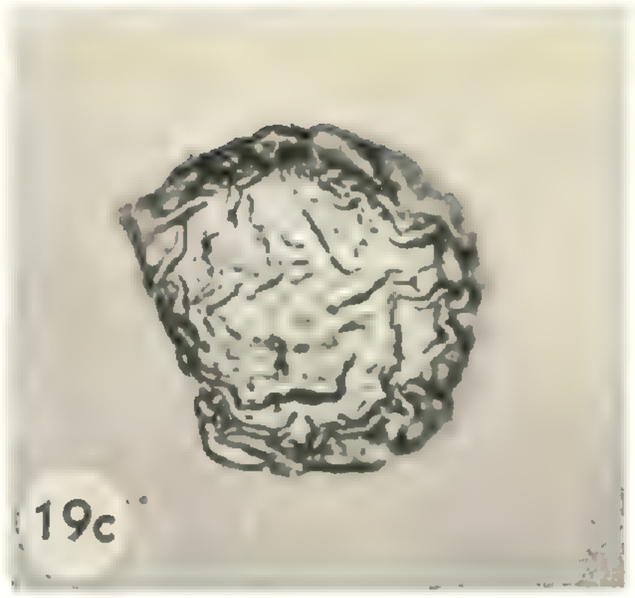


S. SIBIRICA

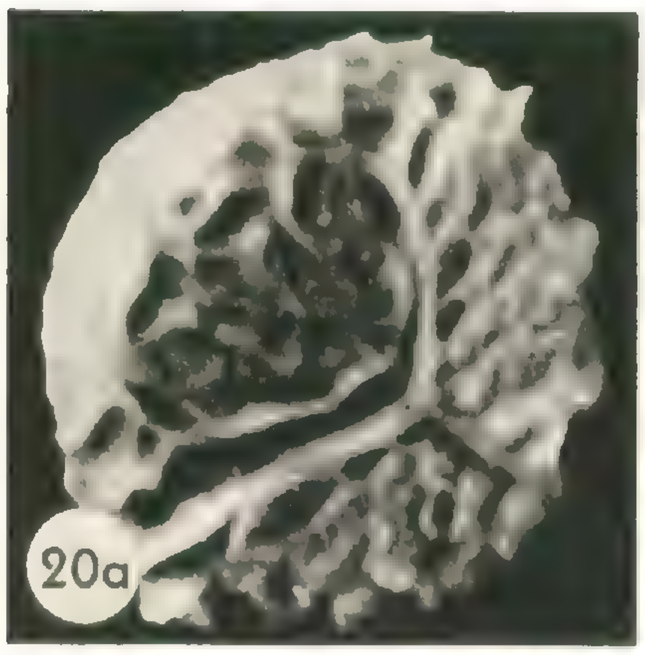
TRYON — SELAGINELLA SPORES

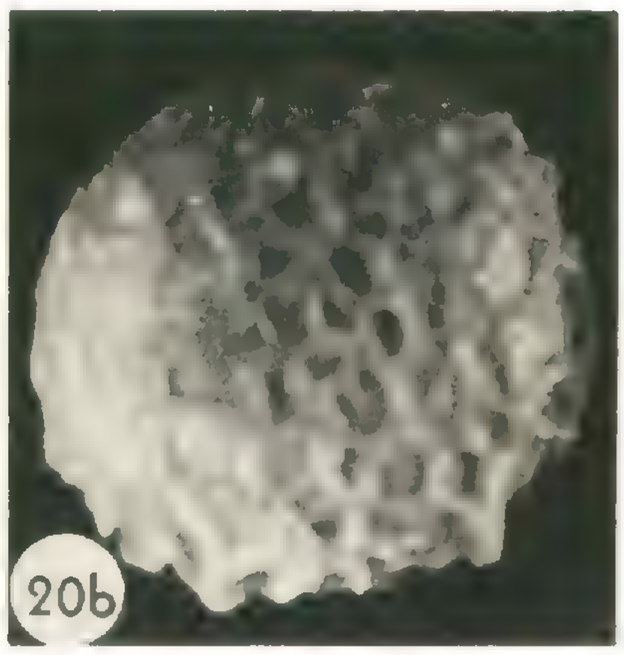




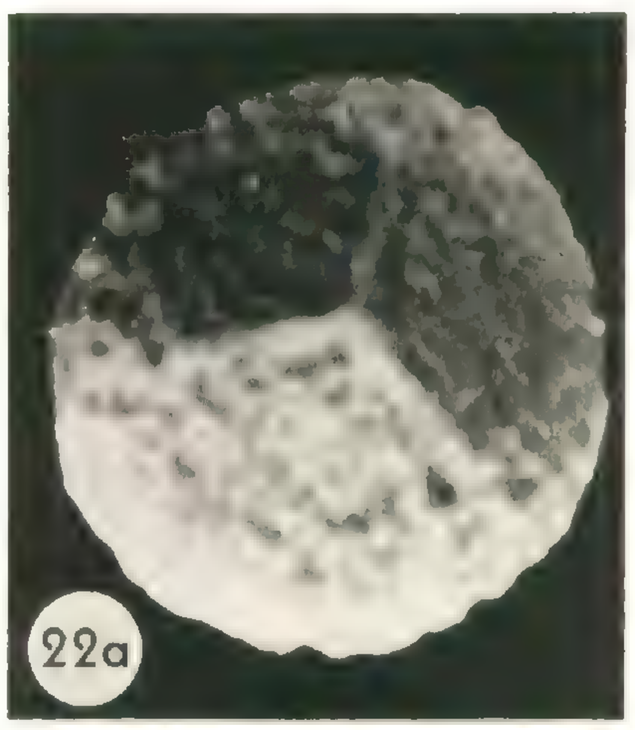


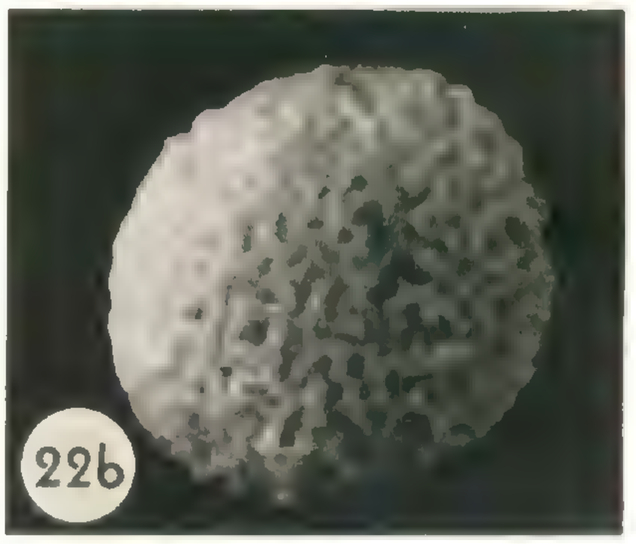
S. ASPRELLA



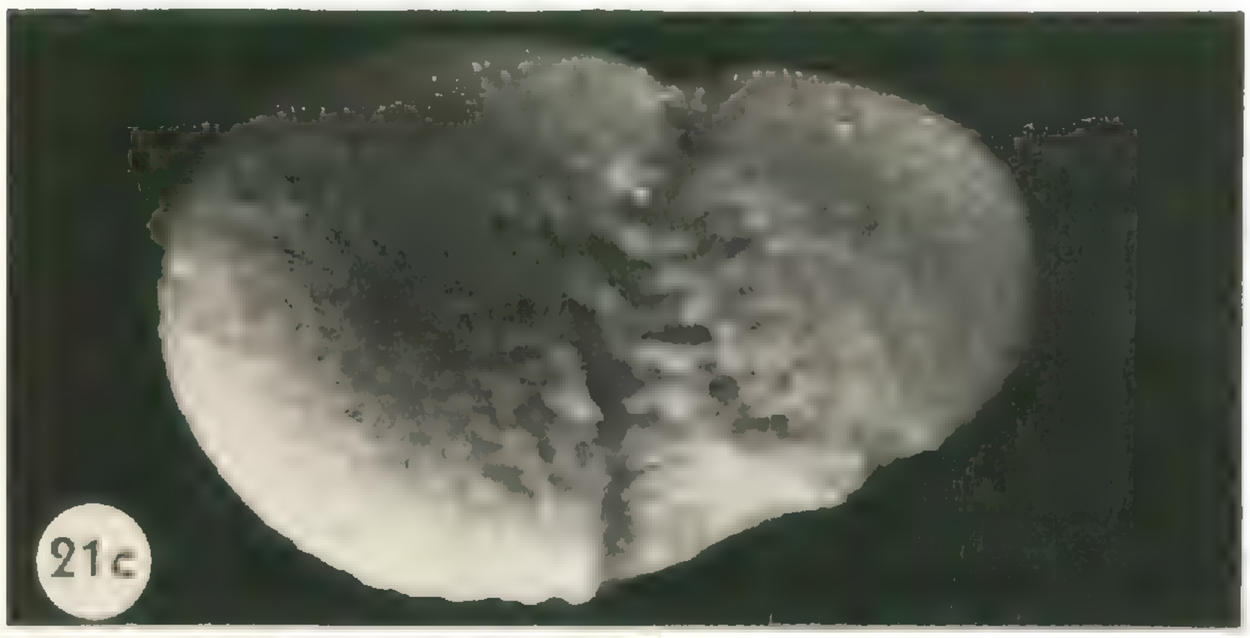


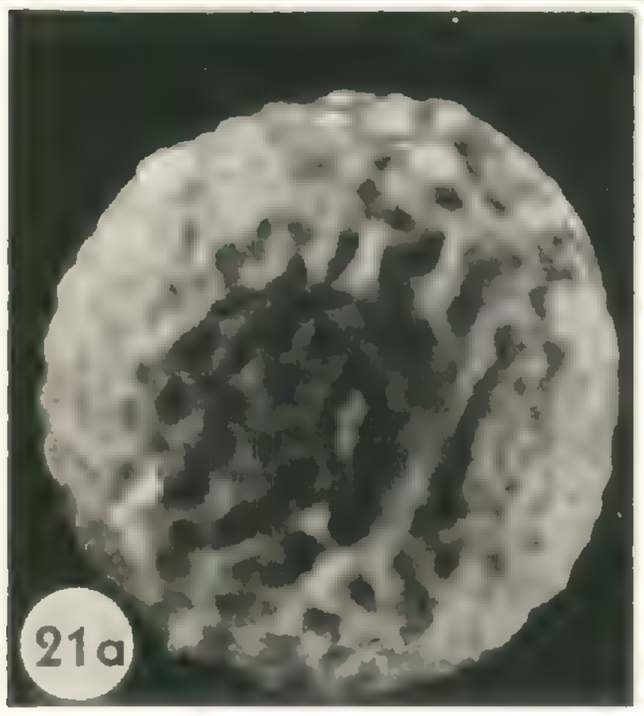
S. DENSA

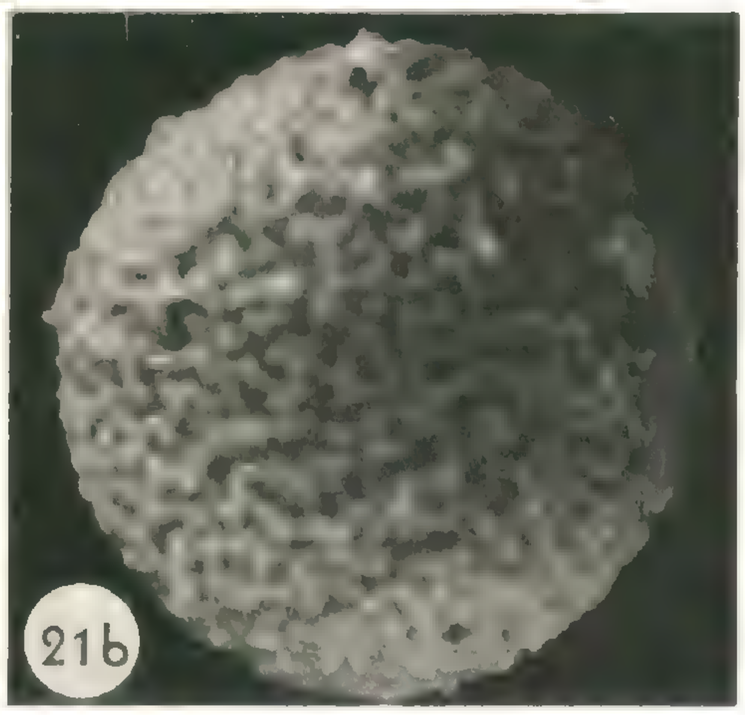


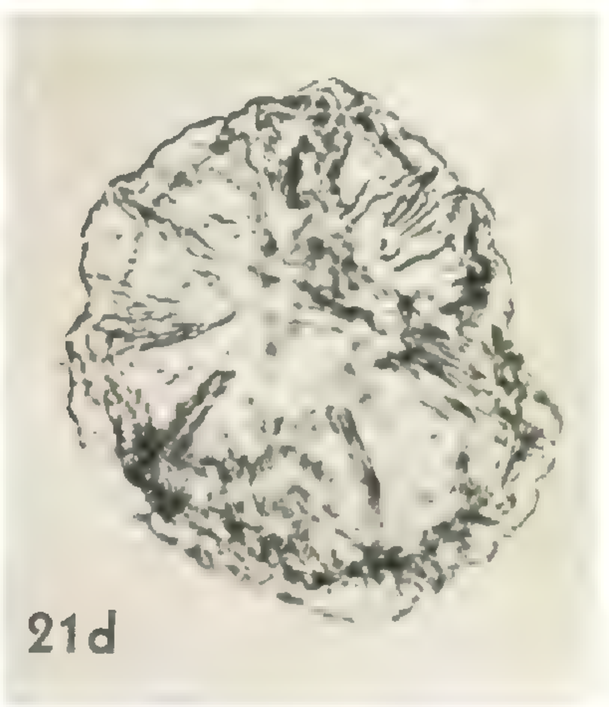


S. SCOPULORUM









S. RUPESTRIS

TRYON — SELAGINELLA SPORES

Explanation of Plate

PLATE 28

Fig. 19. S. asprella: *Johnston 1807*, California, 1917, Paratype (U. S. Nat. Herb.). 19a. Commissural face of megaspore. 19b. Outer face of megaspore. 19c. Microspore.

Fig. 20. S. densa: *Rydberg & Bessey 3517*, Montana, 1897, Isotype (Chicago Nat. Hist. Mus.). 20a. Commissural face of megaspore. 20b. Outer face of prominently marked megaspore.

Fig. 21. S. rupestris: 21a. Commissural face of a megaspore with a single, straight commissural ridge: *B. C. Taylor 1573*, Wisconsin, 1892 (Univ. Minn.). 21b. Outer face of megaspore: *Umbach 5166*, Indiana, 1910 (Mo. Bot. Gard.). 21c. Dumb-bell megaspore, from same specimen as 21a. 21d. Microspore, *Tryon & Tryon 5005*, Wisconsin, 1947 (Mo. Bot. Gard.).

Fig. 22. S. scopulorum: 22a. Commissural face of megaspore, *Shaw 902*, British Columbia, Isoparatype (Univ. Minn.). 22b. Outer face of megaspore, *Umbach 856*, Montana, Isoparatype (Chicago Nat. Hist. Mus.).

Explanation of Plate

PLATE 29

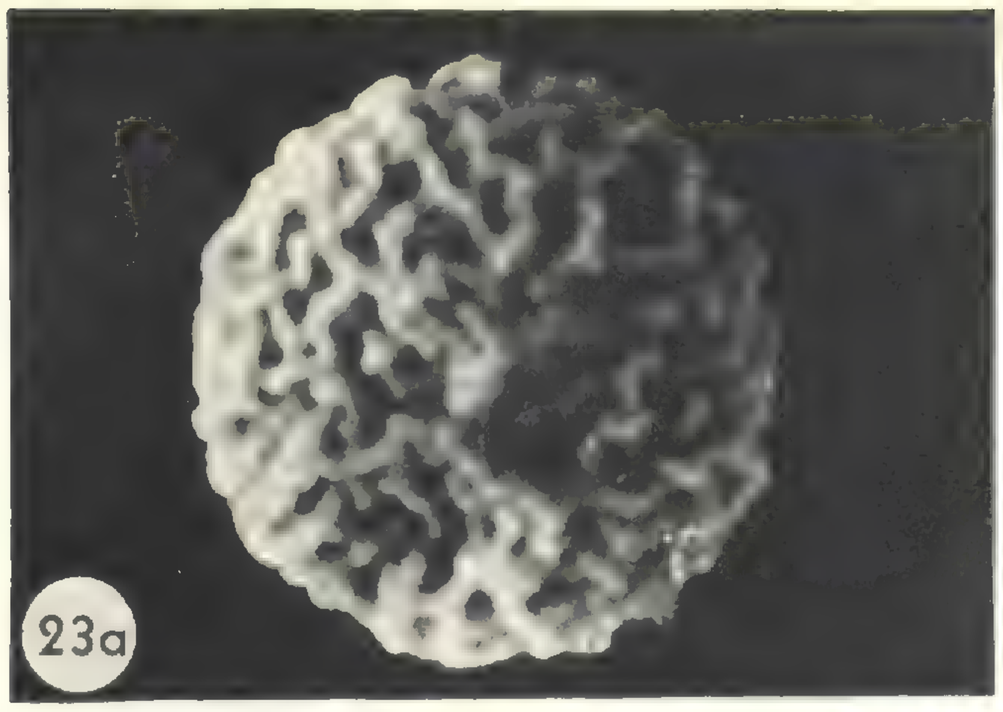
Fig. 23. S. Wrightii: *Reverchon*, Texas, 1883 (U. S. Nat. Herb.). 23a. Commissural face of megaspore. 23b. Outer face of megaspore.

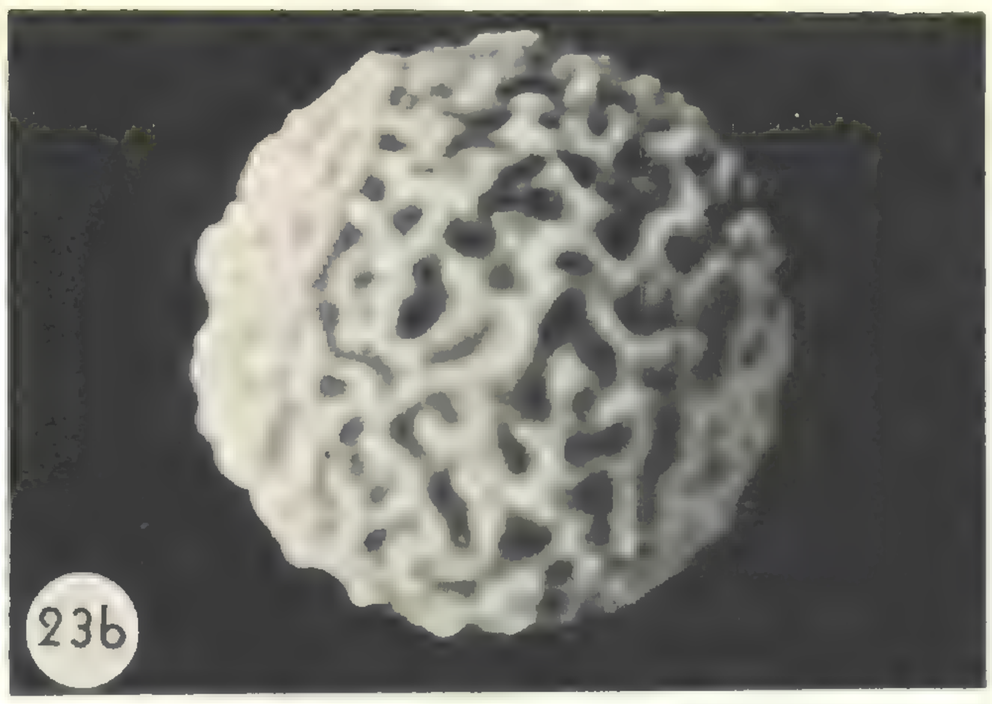
Fig. 24. S. Sheldoni: *Cory 30143*, Texas, 1938 (Mo. Bot. Gard.). 24a. Commissural face of megaspore. 24b. Outer face of megaspore. 24c. Microspore.

Fig. 25. S. Hansini: *Heller 11802*, California, 1915 (Chicago Nat. Hist. Mus.). 25a. Commissural face of megaspore. 25b. Outer face of megaspore.

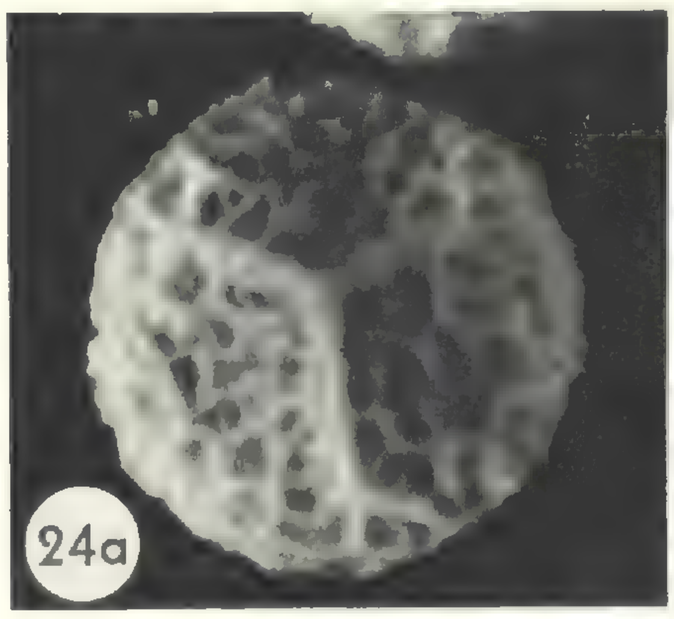
Fig. 26. S. arizonica: *Goodding*, Arizona, 1921 (Chicago Nat. Hist. Mus.). 26a. Commissural face of megaspore. 26b. Outer face of a lightly marked megaspore.

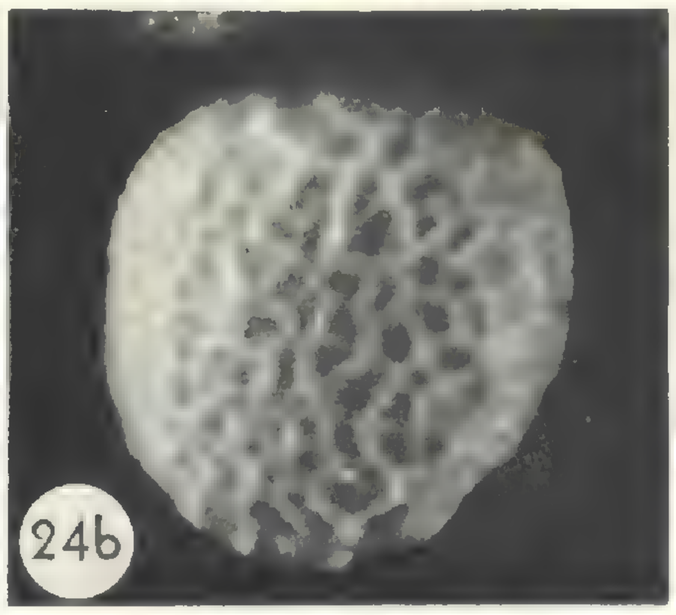
Fig. 27. S. eremophila: *Cook*, California, 1921 (U. S. Nat. Herb.). 27a. Commissural face of a megaspore with obscure equatorial ring. 27b. Outer face of megaspore.

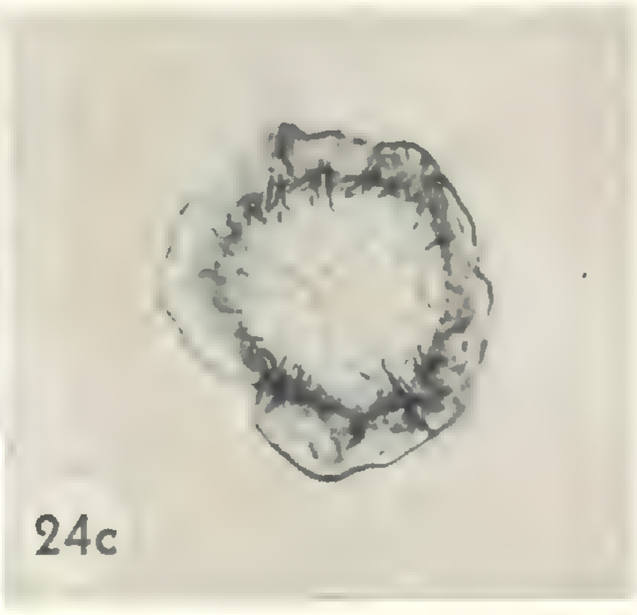




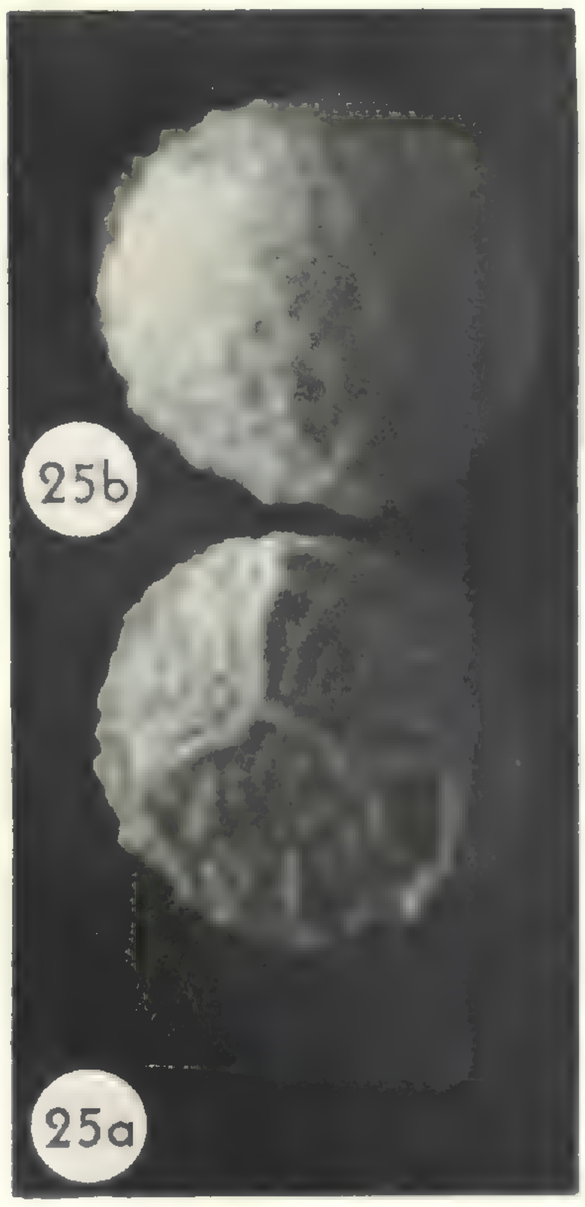
S. Wrightii

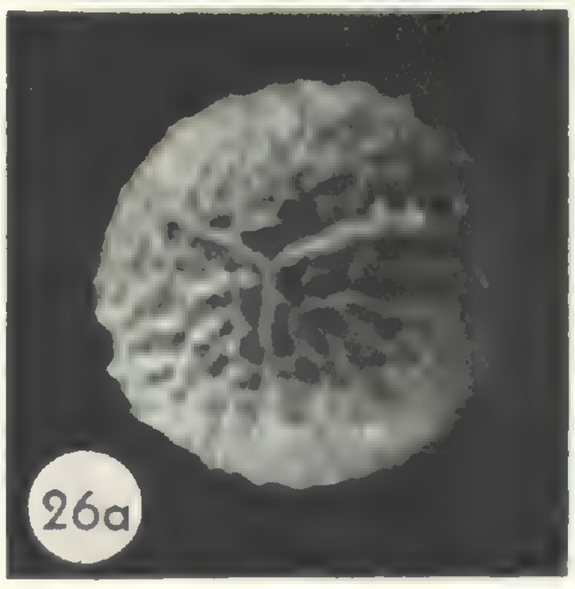


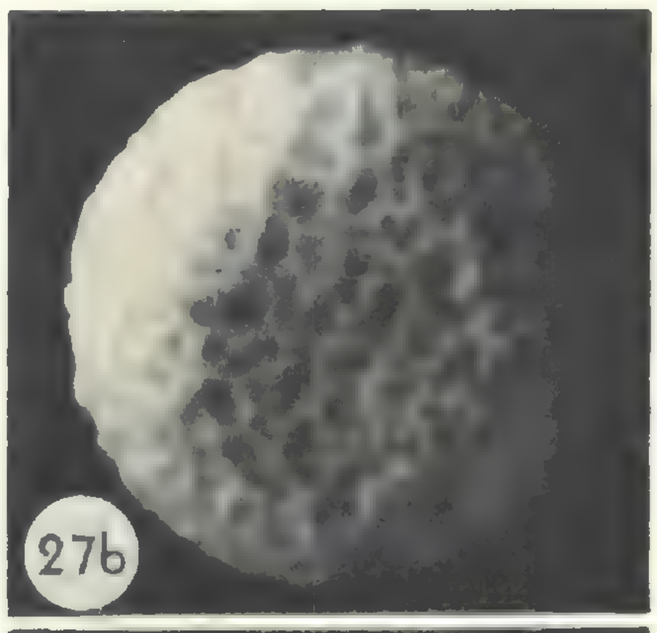


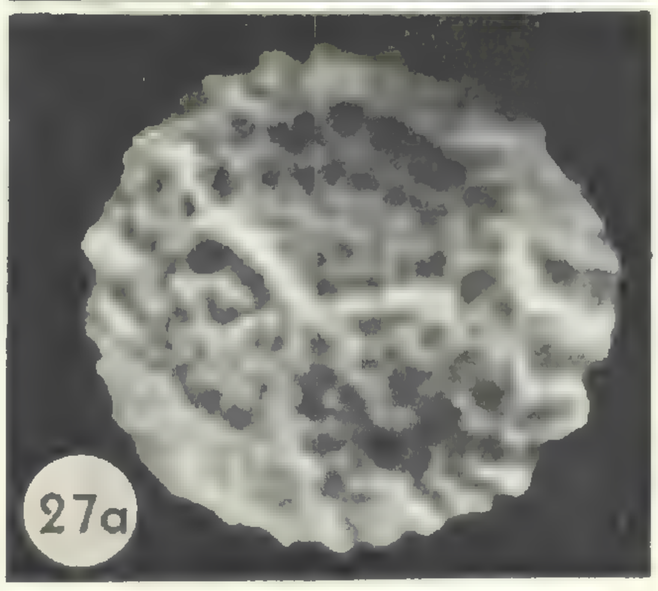


S. Sheldoni



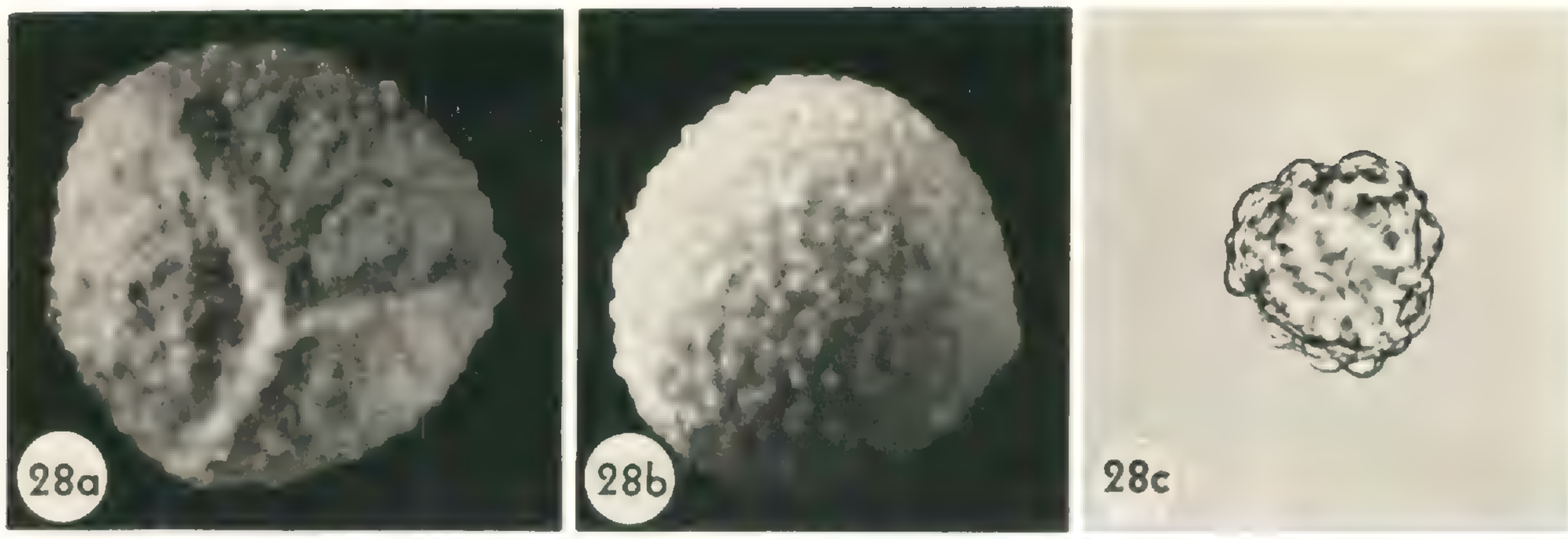




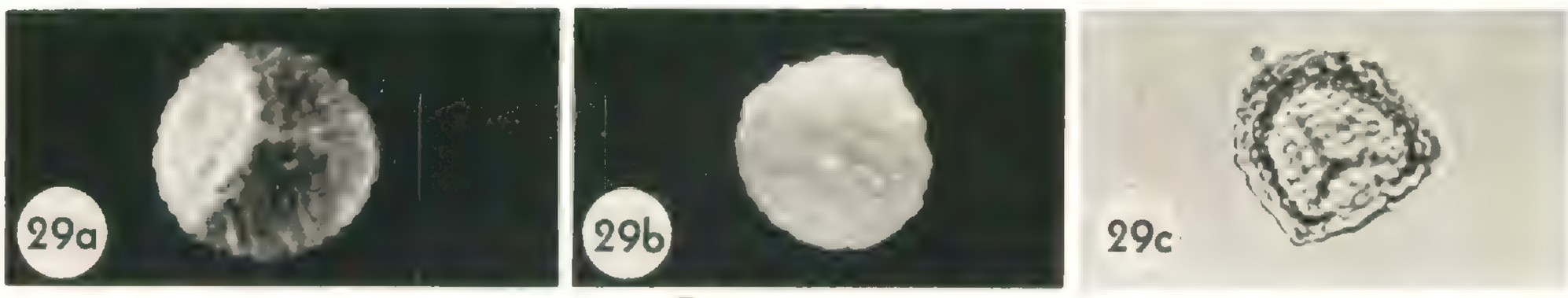


S. Hanseni S. arizonica S. eremophila

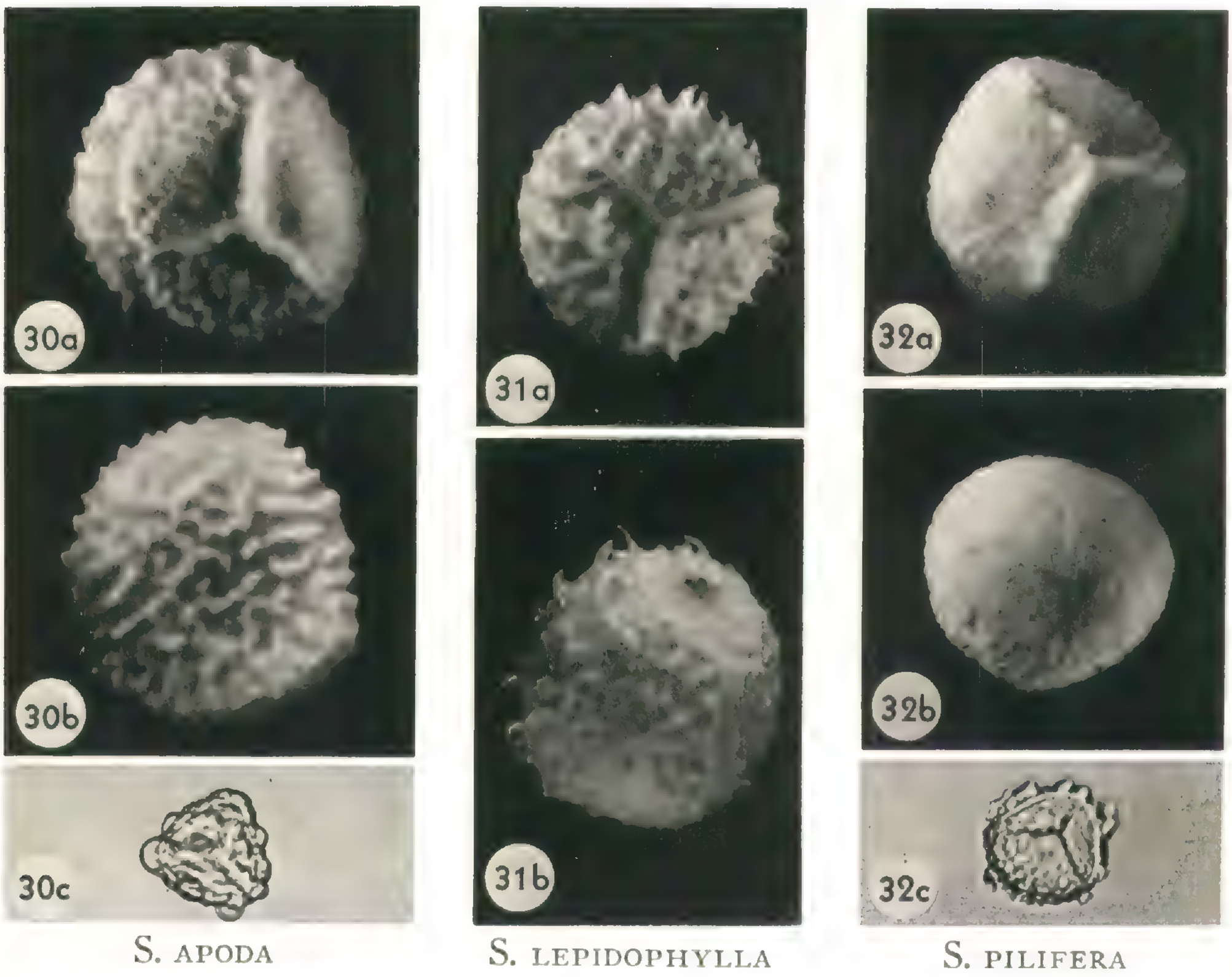
TRYON — SELAGINELLA SPORES



S. DOUGLASII



S. ARMATA



S. APODA S. LEPIDOPHYLLA S. PILIFERA

TRYON — SELAGINELLA SPORES

Explanation of Plate

PLATE 30

Fig. 28. S. Douglasii: *Peck*, Oregon, 1914 (Mo. Bot. Gard.). 28a. Commissural face of megaspore. 28b. Outer face of megaspore. 28c. Microspore.

Fig. 29. S. armata: *Small & Carter*, Florida, 1903 (Univ. Minn.). 29a. Commissural face of megaspore. 29b. Outer face of megaspore. 29c. Microspore.

Fig. 30. S. apoda: 30a. Commissural face of megaspore, *Ruth*, Pennsylvania, 1890 (Univ. Minn.). 30b. Outer face of megaspore, from same specimen as 30a. 30c. Microspore, *E. L. Nielson 1564*, Massachusetts, 1932 (Univ. Minn.).

Fig. 31. S. lepidophylla: *E. J. Palmer 11366*, Texas, 1917 (Mo. Bot. Gard.). 31a. Commissural face of megaspore. 31b. Outer face of megaspore.

Fig. 32. S. pilifera: *C. H. Mueller 8257*, Texas (Mo. Bot. Gard.). 32a. Commissural face of megaspore without equatorial ring. 32b. Outer face of megaspore. 32c. Microspore.

THE CYTOLOGY OF *PAPHIOPEDILUM MAUDIAE* HORT.[1]

HENRY A. McQUADE

Statement of the Problem

The hybrid *Paphiopedilum Maudiae* Hort. is the offspring of *Paphiopedilum callosum* var. *Sanderae* and *P. Lawrenceanum* var. *Hyeanum*. It has been used in relatively few crosses despite its quality, and its offspring have rarely, if ever, been able to exceed it. It was felt that an orchid of such superiority which produced little and often no seed should be examined cytologically to ascertain, if possible, the causes of its sterility. Accordingly, cytological examination was made of the parents and the hybrid and some observations were made on somatic tissues of certain related species.

I. Paphiopedilum Pfitz.

Paphiopedilum was originally incorporated in the genus *Cypripedium* described by Linnaeus. From *Cypripedium* were later extracted the three other genera of the Tribe Cypripedilinae as they are generally accepted today; the residue of the large genus continues under Linnaeus' original designation. The orchid-grower continues to refer to various species of *Paphiopedilum* as "*Cypripedium*," and the confusion oftimes extends to the remaining genera.

Linnaeus arrived at the name *Cypripedium* in an effort to latinize what he thought were the proper Greek words for the "Slipper of Venus." These are Κυπρις (Latin *Veneris*) and *ποδιον (calceus)*. The last, however, does not signify the Latin *calceus*, or shoe, but rather is the word for a small foot. Ascherson[2] changed the generic name to *Cypripedilum* (*pedilum* representing the latinization of the Greek equivalent of *calceolus*), and this was adopted by Pfitzer (1886) and published as such. Buser (1894) has concluded that both names represent the latinization of "very mediocre Greek," but that by virtue of priority *Cypripedium* would be correct. Since Linnaeus had used *Cypripedium* consistently in both 'Species Plantarum' and 'Genera Plantarum' Pfitzer would have no right under present-day rules to suggest a change.

Selenipedium was changed to *Selenipedilum* by Pfitzer in 1886 on the same basis that the change was made in *Cypripedium*. The genus was originally described as *Selenepedium* by Reichenbach filius (1859) who used this spelling consistently. On the basis of priority as determined by the present-day rules of nomenclature, *Selenipedium* is the proper expression.

The use of *Phragmopedilum* rather than *Phragmopedium* suggested by Rolfe (1896) is mandatory today since the genus was published originally as *Phragmopedilum* by Pfitzer. In the same manner *Paphiopedilum* (rather than *Paphiopedium*

---

[1] An investigation carried out at the Missouri Botanical Garden and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Henry Shaw School of Botany of Washington University.

[2] Ascherson, P. Flora d. Prov. Brandenburg, p. 700, *in nota*. 1864.

of Kerchove, 1894, or Rolfe, 1896) takes precedence. The regularity that Rolfe sought for the endings of the generic names within the group, and the change sought by Pfitzer on the basis of derivation are tempered by priority. The following keys to the genera, with necessary modification to generic names, are taken from Rolfe and Pfitzer in that order and are offered for comparison.

ROLFE'S KEY TO ORCHIDEAE (ORCHIDACEAE OF PFITZER)

Suborder DIANDRAE (PLEONANDRAE of Pfitzer)
Tribe CYPRIPIDIEAE (CYPRIPEDILINAE of Pfitzer)
Ovary 3-celled with axile placentas; sepals valvate.
Leaves plicate; perianth persistent; seeds subglobose.....*Selenipedium* Rchb. f.
[3 species in South America and Brazil]
Leaves conduplicate; perianth deciduous; seeds fusiform.....*Phragmopedilum* (Pfitz.) Rolfe
[11 tropical American species]
Ovary 1-celled with parietal placentas; seeds fusiform.
Leaves plicate; perianth persistent; sepals valvate.....*Cypripedium* L.
[about 30 widely scattered species in Europe, temperate Asia, and North America]
Leaves conduplicate; perianth deciduous; sepals imbricate .....*Paphiopedilum* Pfitz.
[46 species in tropical Asia]

PFITZER'S KEY TO ORCHIDACEAE

PLEONANDRAE
Tribe CYPRIPEDILINAE
A. Vernation of the leaves convolute, perigonium marcescent, persisting in the fruit.
a. Ovary trilocular, seed almost spherical with brittle outer coat *Selenipedium* Rchb. f.
b. Ovary unilocular, seed elongate with fragile coat.....*Cypripedium* L.
B. Vernation of leaves duplicate, perigonium deciduous.
a. Ovary trilocular, vernation of sepals valvate, margin of slipper-shaped labellum broadly involute or induplicate.....*Phragmopedilum* (Pfitz.) Rolfe
b. Ovary unilocular, vernation of sepals imbricate, margin of slipper-shaped labellum simple and straight, lightly incurved or recurved.....*Paphiopedilum* Pfitz.

Paphiopedilum callosum (Rchb. f.) Pfitz. and its var. *Sanderae* Hort.—*Paphiopedilum callosum* was described as *Cypripedium callosum* by H. G. Reichenbach filius (1896). It was brought from Siam by Alexandre Regnier, of Paris, in 1885, and very little time elapsed between its importation and the possession of a plant by the Sander's Company of St. Albans in England. It was early recognized as a graceful and vigorous form and was soon in culture wherever there were orchid enthusiasts. (See pl. 31.)

The albino form, variety *Sanderae*, appeared in culture in 1893 or 1894. Whether it flowered for the first time in England or France is a matter of debate; an anonymous article in the 'Journal of Horticulture' of 1912 says that it flowered for the first time in the autumn of 1893 in the collection of R. H. Measures, Esquire, at The Woodlands, Streatham. Be that as it may, in the Seventh Annual Show of the Royal Horticultural Society at the Inner Temple Gardens of May 23–25, 1894, it won a First Class Certificate when exhibited by Messrs. Sander and Sons of St. Albans. Both the Sander's plant and that of Measures appear to have come from the same source.

For several years the variety *Sanderae* remained something of a rarity but came at length to be well represented in collections everywhere; its similarity to the

albino form of *Lawrenceanum* was commented upon but it was considered by most to be more graceful.

Paphiopedilum Lawrenceanum (Rchb. f.) Pfitz. and its var. *Hyeanum* (Rchb. f.)—*Paphiopedilum Lawrenceanum* (see pl. 31) was described as *Cypripedium Lawrenceanum* by H. G. Reichenbach filius in 1878. The plant was found on the bank of the Lawas River by Mr. F. W. Burbidge while on a collecting trip in North Borneo in the service of the Veitch Company. In December, 1878, it was brought to flower in the Veitch greenhouses. Dr. Reichenbach named it for Sir Trevor Lawrence, Baronet, M. P., a contemporary orchid enthusiast whose collection is described as "being of exceptional richness and beauty" (Reichenbach, 1878).

The albino form appeared spontaneously in the Linden cultures of ordinary *Lawrenceanum* which had been imported by Messrs. Lowe & Co. of Clapton. Mr. Jules Hye of Ghent, a fancier, was most eager to secure such a rarity for his own collection, and apparently Mr. Linden, after having sold it to him, decided to name the plant for his customer. It was shown in the April 27, 1886, meeting of the Royal Horticultural Society by two exhibitors, the Compagnie Continetal, and R. B. White, Esquire, of Earlsfield, Surrey.

The new form was at first called *Cypripedium Hyeanum*, by various authors, but it was Reichenbach who first regarded it as a variety.[1] His description appeared in 'Lindenia,' of 1885, changing the nomenclature from *Cypripedium Hyeanum* (L.) Lind. & Rod. to *Cypripedium Lawrenceanum* Rchb. f. var. *Hyeanum* Rchb. f.

× *Paphiopedilum Maudiae* Hort.—The hybrid is a cross between *P. callosum* var. *Sanderae* and *P. Lawrenceanum* var. *Hyeanum*, with the latter as the seed parent (Wilson, 1923). It flowered for the first time in the early fall of 1900 in the houses of Messrs. Charlesworth & Co. of Heaton, Bradford, England, and on September 27 of that year took a First Class Certificate at the Manchester Orchid Society exhibition. A similar award was given when it was shown by Mr. G. W. Law-Schofield at the Royal Horticultural Society on July 30, 1901. Since that time it has been highly prized as a show plant, decorative plant, and commercial orchid. (See pl. 31).

Just who is to be credited with making the cross is a matter of conjecture. It has been reported that it was made in the Charlesworth establishment and again as having been made by two amateur growers, Major Mason and Mr. Charles Winn. In any event, the pot containing the seeds came into the possession of the Charles-

---

[1] Reichenbach (Gard. Chron. 18:748) states: "Mr. Jules Hye Leysen, of Gand, Coupure 8, was so very kind as to send me the only flower we Europeans have had the opportunity of seeing . . . . I immediately thought it might be an albino of Sir Trevor Lawrence's *Cypripedium* . . . . I am persuaded we must regard it as *Cypripedium Lawrenceanum* variety *Hyeanum*, the name having been given, otherwise we might better call it 'Mons. Hye Leysen's individual' . . . . The history is simply, that it was found at the old establishment at Linden amidst a mass of typical *C. Lawrenceanum*."

worth Company which is recorded as having produced the first flower. The plant was named for the daughter of Mr. Baguley, the Charlesworth foreman. The cross, of course, was inevitable since the parent forms were collector's items valued at more than 100 guineas a plant, a price which indicated the value then placed on such desirable forms.

There is a peculiarity in the nomenclature of the hybrid *Maudiae* which should be mentioned. If the specific, rather than the varietal, forms of the parent species had been crossed, the name *Maudiae* would have denoted a colored form. The albino form would then have to be designated by some such additional term as *albescens*. As it happened, × *Paphiopedilum Maudiae* denotes the albino form, and the colored hybrid which appeared six years later had to be designated *P. Maudiae* var. *coloratum*.

From the albino form, several selections have been made. Among them are *P. Maudiae* var. *magnificum*, *P. Maudiae* Westonbirt variety, *P. Maudiae* Dell variety, and *P. Maudiae* Bank House variety.

The interspecific hybrid *Paphiopedilum Maudiae* exhibits hybrid vigor in both growth and flowering, for it is sturdier than either of its parents and flowers more frequently. There are certain striking characters in the hybrid which are readily seen in one parent or the other. The following table compares some of these characters in parents and offspring:

	P. Lawrenceanum	*P. callosum*	× *Maudiae*
Leaves	Tessellated	Marbled	Tessellated
Petals	(a) Horizontal	Pendent or drooping	Intermediate (if otherwise it is closer to *callosum*)
	(b) Tip acute	Acuminate	Acute
	(c) Warted on upper and lower edges	Warted on upper edge only	Warted on upper edge only
Sepals	(a) Warted at base	Not warted at base	Not warted at base
	(b) Somewhat ciliate	Less ciliate	As in *callosum*

In order to clarify the positions of the species within the genus and the appearances of the entities involved, the following outline is added. The system is that of Pfitzer which is at present accepted but the only varieties mentioned are those bearing on this problem. All but the descriptions of *Maudiae* are from Sander's Orchid Guide of 1927.

Genus *Paphiopedilum*

Subgenus: Otopedilum. (There are 3 subgenera. The others are Brachypetalum and Anatopedilum)

Section: Phacopetalum. (There are 11 sections of subgenus Otopedilum)

Species:
1. *P. Curtisii*
2. *P. ciliolare*
3. *P. superbiens*
4. *P. Argus*
5. *P. barbatum*
6. *P. callosum*
   P. callosum var. *Sanderae*
7. *P. Lawrenceanum*
   P. Lawrenceanum var. *Hyeanum*

P. callosum: Foliage marbled. Scape 1 to 2 feet, 1- or 2-flowered. Flowers large, variable, dorsal sepal white, shaded or green at base, striped and often flushed with dark crimson, petals pale green with rose-purple apices, warted and ciliated at upper margins, lip brown-purple. Winter to summer.

Var. *Sanderae:* Dorsal sepal white with apple-green stripes and radiating dorsal veins, petals pale green, whitish on the upper edges, lip pale green. Winter to summer.

P. Lawrenceanum: Foliage brightly tessellated. Scapes 1–2 feet high. Flowers large, bold, dorsal sepal white with purple-red stripes, greenish at base, petals horizontal, greenish with purple shading, chiefly at the tips and margins, black-warted on both edges. Lip dull purple tinted with brown, variable. Summer.

Var. *Hyeanum:* Dorsal sepal pure white with green stripes, petals yellowish green, lip greenish. Summer.

× *P. Maudiae* (Rolfe, 1900): An albino. Dorsal sepal very broad and rounded, white closely veined with bright green. Petals somewhat falcate, light green with darker veins and a few darker warts on the upper margins. Lip and scape light green. Flowering time various.

II. Status of *Paphiopedilum Maudiae* as a Parent Plant

The hybrid *P. Maudiae* combines the winter-flowering habit of one parent with the summer-flowering habit of the other and is one of a small group of albinos within its genus. It is, furthermore, an exceptionally beautiful plant. These features would seem to make it a highly desirable parent yet it has not been used to great extent perhaps because of its sterility. When *Maudiae* has been used in what would appear to be advantageous crosses there has been little seed produced and the extended flowering period characteristic of *Maudiae* has, as a rule, not been obtained in the offspring.

Albino-flowered forms are rare in *Paphiopedilum,* the great majority of species as yet not having produced any. Although there is a considerable number of advanced[1] albino hybrids today, they may be traced back to one or more of these basic forms (Black, 1933; Cooper, 1946).

1. *P. bellatulum* var. *album* and *P. niveum* (subgenus Brachypetalum). These are the only species in which true whites are formed. Even so *P. niveum* shows a faint peppering of purple when viewed closely.

2. *P. Lawrenceanum* (var. *Hyeanum*), *P. callosum* (var. *Sanderae*), and *P. Curtissii* (all in sect. Phacopetalum) have albino forms in which the white is striped and shaded with green. These belong to the "mottled group" characterized by marbled or tessellated foliage and petals ciliated and warted.

3. *P. Charlesworthii* var. *album* (sect. Neuropetalum) which may no longer be in cultivation.

---

[1]In this study the expression primary hybrid is construed to mean species or variety hybrid. An advanced hybrid is one in which one or both parents is of hybrid origin.

4. *P. insigne* vars. *Sanderae* and *Sanderianum* (sect. NEUROPETALUM) is a soft yellow of variable depth according to the form. It is not striped, and white appears in the dorsal sepal. It is the chief member of the "insigne group."

Some success has been achieved by combining *Maudiae* with other albino varieties (Wilson, 1923):

HOLDENII *(Maudiae* × *callosum* var. *Sanderae)*.—Exhibited in 1909.

ALMA GAVAERT *(Maudiae* × *Lawrenceanum* var. *Hyeanum)*.—Flowered in 1911.

WARDEN *(Maudiae* × *Holdenii)*.—Flowered 1920.

EMERALD *(Maudiae* × *Curtissii* var. *Sanderae)*.—Exhibited in 1920.

ENCHANTRESS *(*ALMA GAVAERT × *Curtissii* var. *Sanderae)*.—Exhibited in 1921.

ROSETTII *(Maudiae* × *insigne* var. *Sanderianum)*.—Exhibited in 1908.

Before entering into a discussion of the crosses in which *P. Maudiae* and its parents have been involved, a further breakdown of the genus is necessary. The key given is taken from Pfitzer and may be used in conjunction with Charts I, II and III and their appendices:

KEY TO THE SUBGENERA OF *PAPHIOPEDILUM*

A. Labellum a slipper, exauriculate (without ears or auricles), bag-shaped, having a very short claw at the fore of the narrow inwardly rolled margin; petals very broadly elliptical or almost orbicular; leaves shortly elliptical, tessellated above, more or less purple below, scape uni- or bifloral .....Subgenus 1. BRACHYPETALUM Hallier[1]

B. Labellum a slipper, exauriculate, inclining downward, having a claw of almost equal length to that of the slipper on the front of the simple non-involute margin; petals elongate; leaves strap-shaped, green on both sides, scape several-flowered.....Subgenus 2. ANATOPEDILUM Pfitz.

C. Labellum a slipper, auriculate, bag-shaped, having a claw almost as long as the slipper at the fore of the simple, non-involute margin; petals elongate; leaves varying, scape several or single-flowered ..... Subgenus 3. OTOPEDILUM Pfitz.

KEY TO THE SECTIONS OF THE SUBGENUS ANATOPEDILUM

A. Sepals striate between simple curving nerves; petals deflexed (bent outwardly), elongate with ciliate margins; staminode cylindrical, bent, the lower ascending part with long hair, the upper descending part glabrous above with two lobed apex.. ..Sect. GONATOPEDILUM Pfitz.

B. Sepals striate between simple curving nerves; petals deflexed, elongate, twisted margins adorned with hairy warts; staminode directed upward and forward, arched over, pilose below the concave margin.....Sect. CORYOPEDILUM Pfitz.

C. Sepals with extra striate curving nerves between tenuous reticulate nerves; petals curved, elongate, margin almost naked; staminode like that of the preceding section. ..... Sect. PRENIPEDILUM Pfitz.

KEY TO THE SECTIONS OF THE SUBGENUS OTOPEDILUM

A. Staminode inversely heart-shaped, forked, enlarged on the back by a basal boss, acute, pilose. Leaves strap-shaped, uniform in tint, almost erect, green. Scapes several-flowered, flowering simultaneously.

a. Petals narrow, hanging, often twisted on the lower margin, decorated with hairy warts, minutely spatulate at the apex. Leaves very narrow with hyaline margins.....
.....Sect. MYSTROPETALUM Pfitz.

b. Petals narrow from linear base toward the apex, frequently expanding into a blade, extremely divergent, nearly twisted, margin without warts. Leaves very narrowly yellow-margined .....Sect. PARDALOPETALUM Hallier

[1] *Brachypetalum* is not further divided to sections but is divided directly into species.

B. Staminode lightly forked, almost with an undivided boss at the back. Leaves broadly strap-shaped, recurved, uniform in tint, green or glaucous. Scape several-flowered, bracts emarginate, flowering successively.....Sect. COCHLOPETALUM Hallier

C. Staminode nearly orbicular, square, heart-shaped or almost heart-shaped. Sepals with tenuous reticulate nerves between simple curved nerves. Leaves green, uniform in tint, scapes unifloral, very rarely bifloral.

a. Staminode nearly square, enlarged on the back by 3 low, slightly prominent bosses; petals spatulate.....Sect. STICTOPETALUM Hallier

b. Staminode almost reverse heart-shaped, blunt, enlarged on the convex or plane back by one large central boss; petals more or less expanding into a blade toward the apex.....Sect. NEUROPETALUM Hallier

c. Staminode heart-shaped, furrowed at the back, slightly bossed; petals elliptical. .....Sect. THIOPETALUM Hallier

d. Staminode almost round, split on the posterior with rolled-back lobes; petals oblong with wavy margins.....Sect. CYMATOPETALUM Hallier

D. Staminode half-moon-shaped, the fore part equally three-cusped; sepals with simple curving nerves uniting reticularly at the apex; petals strongly sigmoid, bent outwards at the apex, erect. Leaves green, uniform in tint, scape unifloral..... .....Sect. CERATOPETALUM Hallier

E. Staminode half-moon-shaped, with double horse-shoe-shaped or now and then nearly rhombic boss. Sepals net-veined or simply veined, petals clearly expanding into a blade toward the apex. Leaves more or less tessellate (checkered), scape unifloral.....Sect. SPATHOPETALUM Pfitz.

F. Staminode moon-shaped or semi-rounded, without a boss; sepals simply nerved; petals not expanding or hardly expanding into a blade toward the apex. Leaves clearly tessellate, scape unifloral, rarely bifloral.

a. Petal margins naked or haired with equally disposed cilia..... .....Sect. BLEPHAROPETALUM Pfitz.

b. Petal margins spotted or adorned with prominent warts provided with small brush-like hair tufts.....Sect. PHACOPETALUM Pfitz.

Maudiae has been crossed to members of nine of the eleven sections of the subgenus OTOPEDILUM or to individuals whose antecedents lie within these sections. (It has not been crossed to individuals belonging to sections PARDALOPETALUM or MYSTROPETALUM.) The section contributing the most germ plasm to individuals crossed with *Maudiae* appears to be NEUROPETALUM; PHACOPETALUM, the section from which *Maudiae* stems, and CYMATOPETALUM contribute somewhat less. Individuals emanating from the NEUROPETALUM group were used freely, probably in efforts to combine *Maudiae's* everblooming character with some of the desirable "*insigne*" characters. Only one cross has been recorded with a BRACHYPETALUM species *(niveum)* and one with ANATOPEDILUM *(Rothschildianum* in sect. GONATOPEDILUM*)*. Of the 35 crosses in which *Maudiae* has been used (Sander's List, 1946), 11 have been with species, 3 with primary hybrids, and 21 with advanced hybrids. (See Chart I).

Paphiopedilum callosum has been crossed to members of nine out of the eleven sections of the subgenus OTOPEDILUM, or individuals having their antecedents therein. (It has not been crossed to individuals with a background in MYSTROPETALUM or PARDALOPETALUM). PHACOPETALUM, to which *callosum* and *Lawrenceanum* belong, is the section contributing the greatest number of individuals to these crosses with NEUROPETALUM and others contributing lesser numbers. It has been crossed to all of the species within the subgenus BRACHYPETALUM and with sections CORYOPEDILUM and PRENIPEDILUM of the subgenus ANATOPEDILUM.

Of its 55 crosses, 29 have been with species, 13 with primary hybrids, and 13 with advanced hybrids. (See Chart II and Appendix).

Paphiopedilum Lawrenceanum has been crossed to representatives of all of the eleven sections of Otopedilum. Again, Phacopetalum and Neuropetalum contribute the most germ plasm to the individuals used in these crosses, with other sections contributing lesser amounts. It has been crossed with all the Brachypetalum species and with individuals belonging to two of the sections of the subgenus Anatopedilum (*Gonatopedilum* and *Coryopedilum*). Of the 62 crosses in which *Lawrenceanum* has been involved, 30 have been with species, 17 with primary hybrids, 15 with advanced hybrids. (See Chart III and Appendix).

The only reasonably complete list of orchid hybrids available is Sander's 'Complete List of Orchid Hybrids' (1946). This lists *Maudiae* as having been used in 35 crosses, *Lawrenceanum* in 62, and *callosum* in 55. Of the 35 offspring of *Maudiae* only 7 have been used to produce 41 named offspring of their own. Twenty *Lawrenceanum* offspring have been used in 123 crosses, and 15 *callosum* offspring in 74, with *Maudiae* being the most productive offspring in either case. It must be remembered, however, that Sander's List does not necessarily present a true picture of sterility or fertility. It simply lists the crosses giving rise to named and registered varieties and gives no account whatever of the crosses made wherein the grower considered the result not worth saving. It is thought, however, that most of the early crosses were named and registered since even the poor ones were regarded as having botanical interest.

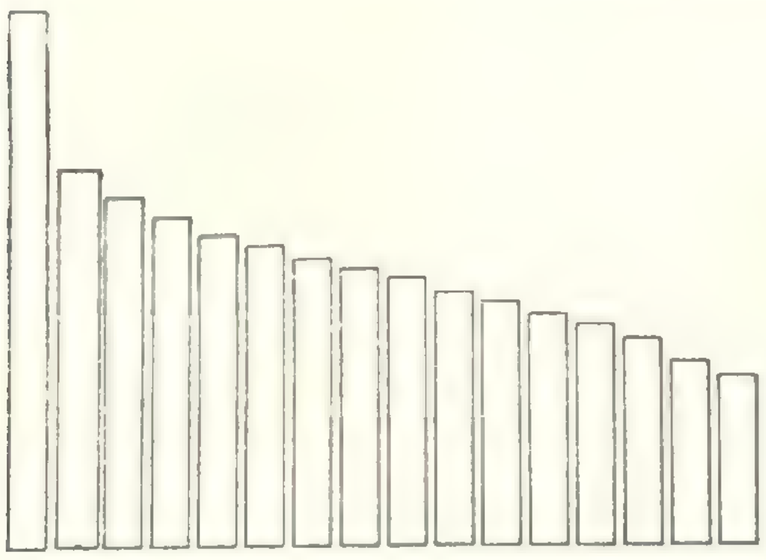
That both *Lawrenceanum* and *callosum* were crossed to more species than *Maudiae* is to be expected since they are older and have been known to horticulturists for a much longer time. It is reasonable to assume from the record that both of these species cross freely with other members of the genus. *Maudiae* appears to be slightly restricted, in comparison to its parents, in the number of sections to which it has been crossed. In part, this restriction may simply be a reflection of the horticulturist's discrimination; crosses made with *callosum* and *Lawrenceanum* that had proved inferior were probably not repeated with *Maudiae*. Also it is to be noted that many of the individuals to which *Maudiae* has been crossed have been advanced hybrids, and this has probably contributed to a lack of seed set. At any rate, hybridizers have not been able to obtain sufficient seed when using *Maudiae* as a parent to combine its undoubted qualities with those of other parents; large numbers of crosses must be made to obtain a small amount of seed.

III. Analysis of Root-Tips

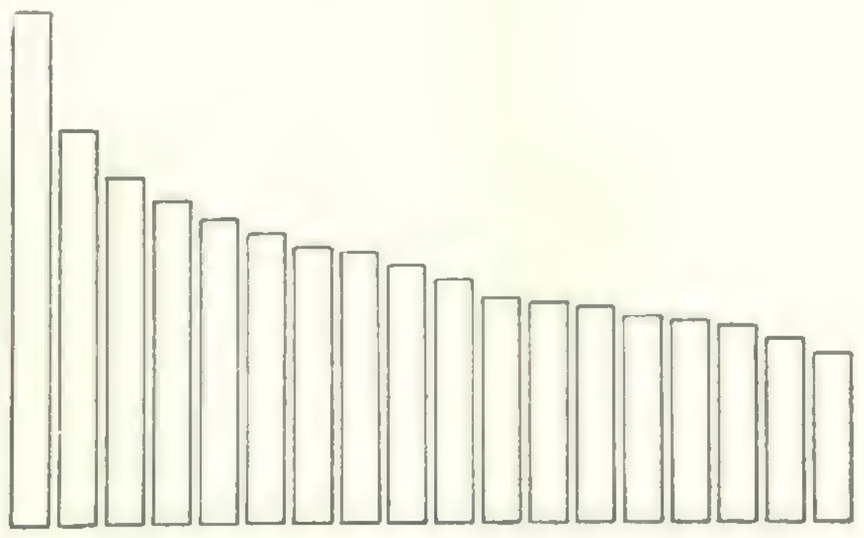
An attempt was made to analyze the chromosome complements of *P. callosum*, *P. Lawrenceanum* (the albino forms were not available), and several forms of × *Maudiae*. For this purpose root-tip smears were used. It was felt that in addition to observation with the microscope and scrutiny of camera-lucida drawings the construction of ideograms would be fruitful. The value of ideograms in this case will be discussed in a following paragraph.

Root-tips were killed and fixed, after quartering, in a solution containing six parts of absolute alcohol to three parts of chloroform to one part of glacial acetic acid. It was necessary to leave the tips in the killing and fixing fluid for at least fifteen minutes although they were often, for reasons of necessity, allowed to remain at least an hour. Tips that could not be squashed and stained immediately after removal from the killing and fixing fluid were kept in an aqueous solution of 45 per cent glacial acetic acid.

The first smears were made from tips of *P. callosum*. Aceto-orcein as well as aceto-lacmoid was used as a stain. After completing observations on *P. callosum* aceto-lacmoid only was used in studying *P. Lawrenceanum* and *P. Maudiae*. The squash procedure used was that outlined by Mehlquist (1947). It was found later in the investigation that the Feulgen technique outlined by Meyer (1943) gave excellent results generally but that for studies involving the centromere region aceto-lacmoid was the best agent when used on root tips that had not been in the Carnoy's fluid for more than fifteen minutes.



Text-fig. 1. *P. callosum*. Comparative length of chromosomes.



Text-fig. 2. *P. Lawrenceanum*. Comparative length of chromosomes.

The construction of ideograms was based upon camera-lucida drawings of mid-metaphase cells so flattened that all parts of a chromosome were in one plane. Ten such plates were obtained for *P. callosum* but only four could be found for *Lawrenceanum* and five for × *Maudiae*. It was the original plan to study ten of each, but, although many root-tips were examined, only this small number was found fit for use. Indeed, it was often difficult to obtain tips showing any divisions at all. On the basis of such small numbers the ideograms are presented here only as indicators and not as final pictures of chromosome complements. Haploid ideograms of *P. callosum* and *P. Lawrenceanum* based upon excellently flattened anaphase cells clearly indicating centromere position are presented. These were not used in the preparation of the final ideograms showing length relationships.

After preparation of camera-lucida drawings, the chromosomes were paired according to length, position of centromere, and placement of secondary constrictions. The basic ideogram thus consisted of the diploid number. For the final ideogram the lengths of the two members of a pair were averaged and the averages of all corresponding pairs were in turn averaged. The final ideogram therefore

shows the haploid number. The haploid ideograms of *P. callosum* and *P. Lawrenceanum* are fundamentally alike. Both show a noticeably long chromosome number 1. The difference in length between chromosomes 1 and 2 is less in *P. Lawrenceanum* than in the other. Aside from chromosome 1 all chromosomes show a very close intergradation in size. (See text-figs. 1 and 2.)

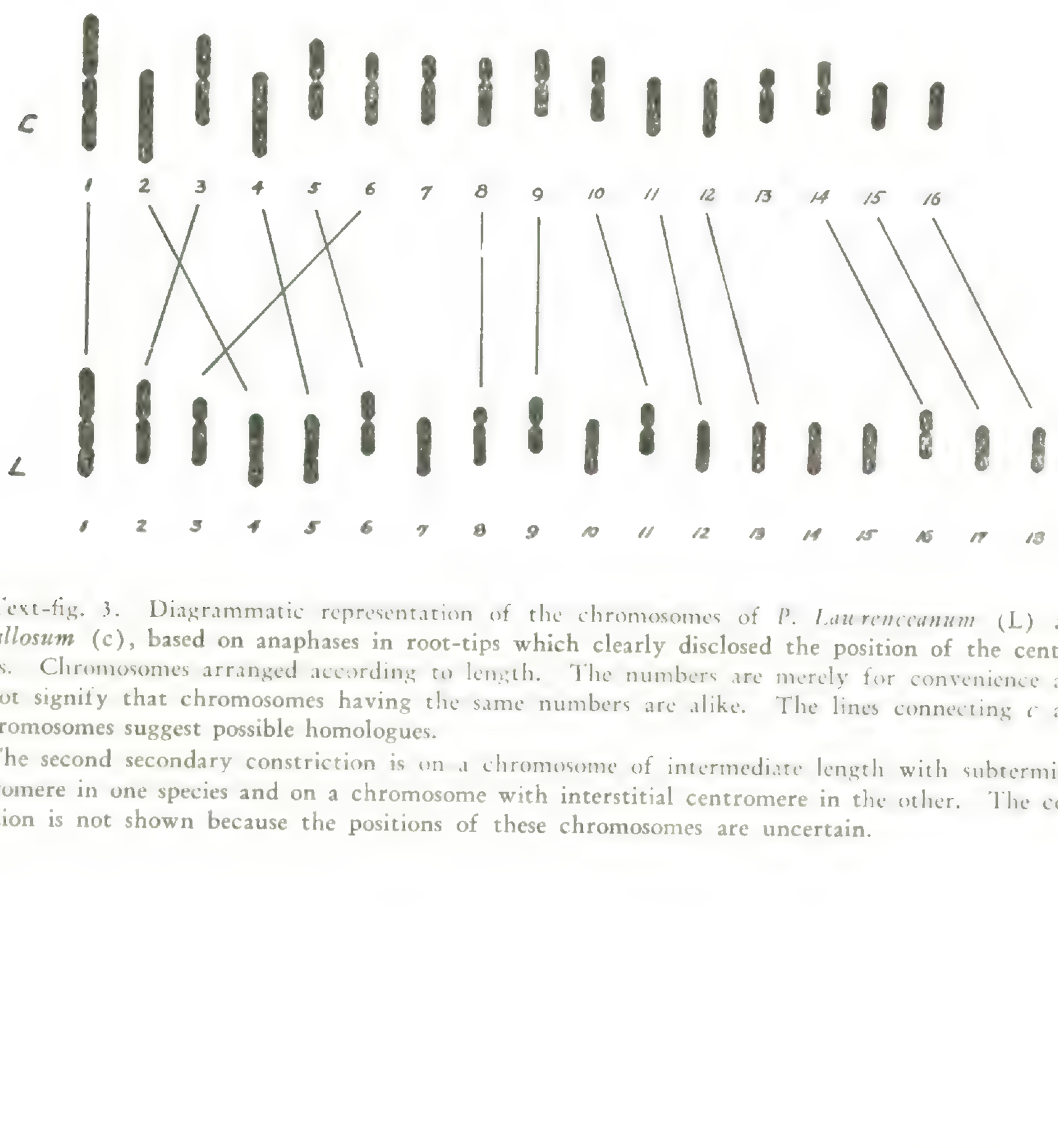
Chromosome counts in various "horticultural Cypripediums," including *P. callosum*, *P. Lawrenceanum*, and the interspecific hybrid *Maudiae*, have been made by Mehlquist (1947a), Duncan (1945, 1947), and others. Some of these counts were verified during this investigation: *P. callosum* has a diploid number of 32; *P. Lawrenceanum*, 36; × *Maudiae*, 34 (see pl. 32); *P. barbatum*, 38; *P. Curtissii*, 36; and *P. superbiens*, 38.

Paphiopedilum callosum, with a 2n number of 32, was analyzed first and ideograms were prepared. All but a few of the sixteen pairs of chromosomes have no identifying morphological features and exhibit a subtle intergradation in lengths. The following chromosomes are best recognized at sight:

1. The longest pair has median centromeres; the secondary constriction is about midway on one arm.

2. A pair intermediate in length often appears to be composed of three pieces of chromatin to each individual. An end piece is a satellite.

3. One pair, longer than average, each with one ball type end, appears to have subterminal centromeres.



Text-fig. 3. Diagrammatic representation of the chromosomes of *P. Lawrenceanum* (L) and *P. callosum* (c), based on anaphases in root-tips which clearly disclosed the position of the centromeres. Chromosomes arranged according to length. The numbers are merely for convenience and do not signify that chromosomes having the same numbers are alike. The lines connecting *c* and *L* chromosomes suggest possible homologues.

The second secondary constriction is on a chromosome of intermediate length with subterminal centromere in one species and on a chromosome with interstitial centromere in the other. The constriction is not shown because the positions of these chromosomes are uncertain.

4. One, or possibly two, pairs shorter than the average, with one ball type end, appears to have subterminal centromeres.

The remaining chromosomes are so alike morphologically and vary so little in length that they cannot be identified as individuals upon observation. However, it can be shown that within the *callosum* complement there are six terminal or subterminal pairs and ten pairs in which the centromeres are interstitial. (See text-fig. 3.)

The chromosomes of *P. Lawrenceanum*, by virtue of their similarity, remain as cryptic as those of *P. callosum*. Here the longest pair is readily identified by having a median, or close to median, centromere and is seen to possess a secondary constriction. Even the smallest chromosomes of *Lawrenceanum* cannot be distinguished readily because of their great similarity in length to the next smallest pair. Thus, aside from the longest pair, the remaining seventeen pairs verge closely on one another in size. The difference in the chromosome numbers of *P. callosum* and *P. Lawrenceanum* appears to be in an increase of small chromosomes in the complement of *P. Lawrenceanum*. It can be shown that in *P. Lawrenceanum* there are ten pairs of terminal or subterminal chromosomes and eight pairs in which the centromeres are interstitial. (See text-fig. 3.)

The chromosomes of the interspecific hybrid *Maudiae* presented the same morphological anonymity as those of the parental forms. Again the long pair with median centromere and clearly defined secondary constriction was readily noted. There are two pairs longer than the average with centromeres between the median and subterminal points, and two pairs of average length with median centromeres but these are not often readily discernible.

The satellited pair of intermediate length seen in *callosum* was seen in *Maudiae* and presented an interesting situation. In regard to this chromosome, *Maudiae* var. *magnificum* is visibly an inversion heterozygote. A cell was found in which it was apparent that half of one of the chromosomes of this pair is inverted. The inverted half bears the centromere, and since the centromere is subterminal in one, it becomes interstitial in the other.

The 2n chromosome configuration of *Maudiae* should consist of 10 chromosomes with terminal or subterminal centromeres and 8 with interstitial centromeres from the *Lawrenceanum* parent, while of the 16 chromosomes contributed by *callosum* 6 should be terminal or subterminal and 10 would be interstitial. Attempts to construct an ideogram showing the diploid number were not rewarding. It may be assumed from these attempts, however, that the close intergradation of chromosome lengths which characterize the parents is characteristic of the offspring.

The value of the ideograms in the analysis of these chromosome complements would appear to be at best only moderate. Ideograms can be used only as approximations for various reasons:

1. The lengths of members of a chromosome pair are not always equal; the longest chromosomes in the basic ideograms, for example, rarely agree exactly in

length. This may be a result of a squashing which leads to distortion not only in length but in other dimensions.

2. Lengths of chromosomes vary from metaphase to metaphase.

3. The length ratio of one pair to another may vary from one metaphase to another because of pressure applied in squashing.

4. The order of 16, 17 or 18 pairs in an ideogram must undoubtedly differ to some degree when there are many of approximately the same lengths lacking distinct morphological features and have been, in addition, subjected to pressure.

5. Centromeres may vary in size or become so small as to be apparently lacking.

6. Satellites vary in size as do also the portions of a multi-piece chromosome.

7. A chromosome may break under pressure not only at the centromere but at other regions. Thus a chromosome could appear to have a median centromere when it is actually of the subterminal type, or a median type, when broken in two, appear to be two subterminal chromosomes.

Despite these reasons for not placing too much faith in the ideogram as an actual picture of the chromosome complement there was sufficient resemblance among the basic ideograms to predict with considerable accuracy the appearance of the final ideogram.

Ideograms of the haploid numbers of various *Paphiopedilum* species published to date by Duncan and MacLeod (1948a, 1948b) include representatives of subgenera BRACHYPETALUM and ANATOPEDILUM and of the sections of OTOPEDILUM except SPATHOPETALUM, BLEPHAROPETALUM and PHACOPETALUM. These, for the most part, indicate a chromosome number 1 recognizable by its length and possessing a median or near median centromere. Chromosome number 2 may approximate or nearly approximate it in length but there is usually a difference. From chromosome number 2 on there is a close intergradation in length down to the smallest chromosome. In this they agree with ideograms published earlier by Francini (1931, 1932, 1934). Among the intermediate chromosomes there is one with a secondary constriction. These same generalities are true for the chromosomes of *P. callosum*, *P. Lawrenceanum*, and *P. Maudiae*, except that these three appear to have an additional secondary constriction on chromosome number 1. Only one species, *P. exul*, ideogrammed by Duncan and MacLeod, shows a secondary constriction on number 1 and none on any other chromosome. (Two species ideogrammed by Duncan and MacLeod exhibit a secondary constriction on number 2 and on no other chromosomes. These are *P. Druryi* and *P. Spicerianum*.)

The following list presents the 2n chromosome numbers to date of species within the genus:

CHROMOSOME NUMBERS OF SPECIES OF PAPHIOPEDILUM

	Chromosome Numbers	Authority*	Date
Subgenus BRACHYPETALUM Hallier			
P. bellatulum (Reichb. f.) Pfitz.	26	D	'47
	26	GM	'47
P. concolor (Batem.) Pfitz.	26	D&ML	'48
P. niveum (Reichb. f.) Pfitz.	26	GM	'47
	26	D	'47
P. Delanatii Guill.	26	D	'47
	26	GM	'47
Subgenus ANATOPEDILUM Pfitz.			
Sect. GONATOPEDILUM Pfitz.			
P. Rothschildianum (Reichb. f.) Pfitz.	26, 28	D	'47
	26	D&ML	'49
Sect. CORYOPEDILUM Pfitz.			
P. praestans (Reichb. f.) Pfitz.	28	D	'47
	28	D&ML	'49
P. philippinense (Reichb. f.) Pfitz.	26	D&ML	'49
Sect. PRENIPEDILUM Pfitz.			
P. Stonei (Hook. f.) Pfitz.	26	D	'47
MARY REGINAE Hort.	26	D&ML	'49
Subgenus OTOPEDILUM Pfitz.			
Sect. MYSTROPETALUM Pfitz.			
P. Parishii (Reichb. f.) Pfitz.	26	D	'47
	26	D&ML	'49
Sect. PARDALOPETALUM Hallier			
P. Lowii (Lindl.) Pfitz.	26	D	'47
	26	D&ML	'49
P. Haynaldianum (Reichb. f.) Pfitz.	26	D	'47
	26	D&ML	'49
Sect. COCHLOPETALUM Hallier			
P. Chamberlainianum (O'Brien) Pfitz.	26	D	'47
P. glaucophyllum J. J. Smith	36	D	'47
Sect. STICTOPETALUM Hallier			
P. hirsutissimum (Lindl.) Pfitz.	26	D&ML	'49
Sect. NEUROPETALUM Hallier			
P. villosum (Lindl.) Pfitz.	26	F	'34
	28	F	'31
	26	GM	'47
	26	D	'47
	26	D&ML	'48
P. Boxallii (Reichb. f.) Pfitz.	26	GM	'47
	26	D&ML	'48

* The abbreviations used for authorities are: D, Robert E. Duncan; D&ML, Robert E. Duncan and Raymond A. MacLeod; F, Eleanora Francini; GM, Gustav A. L. Mehlquist.

	Chromosome Numbers	Authority*	Date
P. insigne (Wall.) Pfitz.	32	F	'31
	26	GM	'47
	26	D	'47
	26	D&ML	'48
P. exul (O'Brien) Pfitz.	26	D	'47
	26	D&ML	'49
P. Charlesworthii (Rolfe) Pfitz.	26	D	'47
	26	D&ML	'49
P. Gratrixianum Rolfe	26	D	'47
	26	D&ML	'48
Sect. THIOPETALUM Hallier			
P. Druryi (Bedd.) Pfitz.	26	D	'47
	26	D&ML	'49
Sect. CYMATOPETALUM Hallier			
P. Spicerianum Pfitz.	30	F	'31
	28	D	'47
	28, 30	D&ML	'49
Sect. CERATOPETALUM Hallier			
P. Fairrieanum (Lindl.) Pfitz.	26	D	'47
	26	GM	'47
	26	D&ML	'49
Sect. SPATHOPETALUM Pfitz.			
P. venustum (Wall.) Pfitz.	36	F	'31
	42	D	'47
Sect. BLEPHAROPETALUM Pfitz.			
P. tonsum (Reichb. f.) Pfitz.	34	D	'47
P. Mastersianum (Reichb. f.) Pfitz.	32	D	'47
P. javanicum (Reinw.) Pfitz.	36	D	'47
P. Dayanum (Reichb. f.) Pfitz.	34	D	'47
P. Wardii Summerhayes	40-45	D	'45
Sect. PHACOPETALUM Pfitz.			
P. Curtisii (Reichb. f.) Pfitz.	36	D	'47
	36	GM	'47
P. superbiens (Reichb. f.) Pfitz.	38	D	'47
P. barbatum (Lindl.) Pfitz.	32	F	'31
	38	F	'34
	38	D	'47
	38	GM	'47
P. callosum (Reichb. f.) Pfitz.	32	D	'47
	32	GM	'47
P. Lawrenceanum (Reichb. f.) Pfitz.	36	D	'47
	36	GM	'47

IV. MEIOSIS

Aceto-lacmoid and aceto-orcein gave metaphase I smear preparations which were clear enough to determine the nature of pairing but the outlines of the chromosomes were often not sharply defined. A modification of the Feulgen technique, although somewhat better, gave much the same result. These methods also proved unsatisfactory for a study of the prophase chromosomes; all of these methods seemed reasonably good for material in anaphase I or later stages. The difficulty was not remedied even when an iron aceto-carmine mordant was added to the Carnoy's Fluid used for killing and fixing. The situation was further complicated by restrictions on the number of buds available; forty were used in the course of the study of pollen mother cells. It must be remembered that none of the plants involved are frequent bloomers, the parental forms blooming once yearly and *Maudiae* at most twice.

It was found after considerable experimentation that the best preparations were obtained by making permanent slides. Anthers were dropped in Carnoy's Fluid for 10–15 seconds and then put in CRAF for 24 to 48 hours. They were then washed and run through the usual tertiary butyl alcohol series and, after infiltration, were embedded. Sections were cut at 10 μ and then stained in crystal violet and safranin (Stockwell, 1934). This method gave results in pachytene and early diplotene which could not be obtained with the smear methods mentioned above, and the metaphase chromosomes were sharply outlined. A peculiarity in the staining effect was noted with the use of crystal violet and safranin. When the slides were left in the stain for a long time both meiotic and mitotic chromosomes were stained dark purple. When exposed to the stain for about 15 minutes the meiotic chromosomes were red while the mitotic nuclei or chromosomes were blue. At an exposure of about 12 minutes both meiotic and mitotic chromosomes were red.

No satisfactory study of chiasmata was made because of the extremely reduced size of the bivalents at mid-metaphase and because the procedure adopted does not spread the chromosomes sufficiently as the smear method so often does. Diakinesis, a stage favorable for the study of chiasmata in many other plants, could not be prepared suitably by any of the methods cited above.

P. Maudiae Hort. var. *magnificum* furnished most of the hybrid material studied although WESTONBIRT and DELL varieties were examined; the last do not appear to differ from *magnificum*.

PAPHIOPEDILUM CALLOSUM (2n = 32)

Prophase I.—Pairing appears to be normal when viewed in the pachytene stage.

Permanent preparations of diakinesis in *callosum* resemble those of *Maudiae* prepared by aceto-lacmoid smears or the Feulgen technique. Within the various techniques employed in this study it may be said that diakinesis in the two species and the hybrid is not a favorable stage for study. The chromosomes appear to be in a fluid or somewhat fluid state and are therefore poorly defined by the stain; large patches of chromatin are occasionally seen where the chromosomes appear to

have stuck together. This perhaps represents a time when the matrix is being elaborated most freely and is therefore quite thin in consistency. Some chiasmata can be seen but no accurate over-all picture can be given. Occasionally they appear as relatively colorless strands between the ill-defined chromosomes and again they appear to be surrounded with enough matrix to render them stainable. Among the chromosomes of intermediate length, two ring configurations have been noticed: one with no free ends and another in which one of the chiasmata is apparently not terminalized so that a short portion of one end of each chromosome is free. The same pair may be involved in both cases. Among the shortest chromosomes (at least those with subterminal centromeres) bivalents are formed with only one chiasma. The longest pair appears to form three or four chiasmata. The nucleolus is plainly visible at diakinesis.

Metaphase I.—Metaphase chromosomes have not been stained as clearly as desired by smear methods but were clear enough to determine pairing; chiasmata could not be properly interpreted. Twenty-five metaphase cells examined showed pairing to be in 16 bivalents. (See pl. 32).

Of 114 metaphase plates seen in side view, 107 appeared to have all their chromosomes in the plate in the normal fashion. One cell appeared to have one lagging chromosome, 2 were doubtful as to fragments or isolated chromosomes, and 5 appeared to have isolated chromosomes or fragments in each. It is entirely possible that these apparent abnormalities existed as a result of smearing.

Anaphase I.—Fifty-six anaphase cells were examined and no anaphase bridges were observed. One cell appeared to have a fragment between the two poles. Anaphase appears to be normal.

Telophase I.—No cell wall is formed at the close of division I. An interphase nucleus is formed.

Telophase II.—Five hundred tetrads were examined. No micro-grains or small extra cells were found within the thick wall.

Pollen grains.—Pollen grains were mounted in aceto-lacmoid for staining but were not pressed. The grains are elliptical to spherical in shape. Of 500 grains examined only 8 were found to be empty; no shrunken or distorted grains were found. The grains are slightly smaller than those of *P. Maudiae*. (See section on pollen grains, × *Paphiopedilum Maudiae*).

PAPHIOPEDILUM LAWRENCEANUM (2n = 36)

Prophase I.—No leptotene or zygotene nuclei have been studied but pachytene and early diplotene nuclei have been observed. The crystal violet-safranin technique was used. Pairing as observed in pachytene appears to be regular throughout and no abnormalities were noticed. The early diplotene stages examined show the initial repulsion between the paired chromosomes.

Metaphase I.—Only 2 metaphase I cells suitable for study were found. These indicated pairing to be in 18 bivalents.

Anaphase I.—Observations on a large number of these cells indicate no apparent abnormalities. Bridges are not formed nor do there appear to be any lagging chromosomes or fragments in evidence. The chromosomes do not appear to be split in readiness for division 2 at this stage.

Telophase I.—An interphase nucleus is formed at this stage but no cell wall is formed. Eighteen chromosomes were counted at one pole in an early telophase.

Metaphase II.—Examination of metaphase II cells indicated that division had been regular. The regularity with which 18 chromosomes are disposed to each pole serves as additional evidence that 18 bivalents are formed at metaphase. (See pl. 32).

Anaphase and Telophase II.—No abnormalities are evident and the tetrads formed resemble those of *P. callosum*. A tetrad was found in which 18 chromosomes could be counted at one pole.

Pollen grains.—Pollen grains are elliptical to spherical and about the same size as the *callosum* grains. Of the 500 grains examined, only 2 were found to be empty. (See section on pollen grains, × *Paphiopedilum Maudiae.*)

× *PAPHIOPEDILUM MAUDIAE* Hort. (2n = 34)

Prophase I.—In the pachytene of *P. Maudiae* the nucleolus appears as a well-defined almost colorless body in intimate contact with chromosomal material. Although in sectioning the knife may frequently remove the nucleolus from cells, it is visible nonetheless in many others. Its attachment to a chromosome is noticeable. It is impossible to tell which chromosome is involved since the pachytene nucleus represents a tangle of long slim threads whose ends, except in chromosomes cut through by the knife, are often not visible. As with *callosum* and *Lawrenceanum* two nucleoli are occasionally visible in the mitotic cells forming the jacket around the pollen mother cells but only one nucleolus has been seen in the PMC's. The nucleoli seen in the PMC's are larger than those seen in mitotic cells.

There have been observed in the pachytene and pachytene-early diplotene chromosome configurations which suggest inversion and deletion but the chromosomes are so attenuate and the suspected loops or buckles so small that it has been impossible to ascertain this. The presence of inversion loops in pairing is to be expected in view of the presence of anaphase bridges.

As in *Lawrenceanum* the beadlike effect of the chromomeres is evident at this stage.

Metaphase I.—The staining with smear methods was suitable enough to examine pairing. Of the 27 metaphase cells of *P. Maudiae* examined, 26 showed 17 bivalent chromosomes. (See pl. 34). One cell showed 16 bivalents and 2 univalents. It appears that two of the *Lawrenceanum* chromosomes are pairing.

Anaphase I.—A total of 483 anaphase I cells were examined and several abnormalities were found:

a. Cells with 1 bridge but no fragments	17
b. Cells with 2 bridges but no fragments	1
c. Cells with 1 bridge and 1 fragment	13
d. Cells with 1 bridge and 2 fragments	1
e. Cells with 2 bridges and 1 fragment	2
f. Cells with 1 fragment (or small isolated chromosome)	15
TOTAL	49

Of the cells examined 10.1 per cent showed abnormalities.

A further analysis of anaphase I was made possible through the observation of 4 cells in which the chromosomes could be counted at one or both poles. While this number is far too small to be regarded as significant the information is included to amplify the notes above.

1. Two cells showed clearly 17 chromosomes at one pole but a count could not be made at the other pole. There were no lagging chromosomes in evidence. The chromosomes were split in readiness for division 2 but this partial separation may have been caused by smearing.

2. One cell showed 17 chromosomes at one pole and 16 at the other. One chromosome lagged but appeared to be slightly closer to the pole with 17. Again the chromosomes were split.

3. One cell had 17 chromosomes at each pole; these were split for division 2.

Tetrads.—Examination of 527 tetrads was made. The arrangement is primarily that of 2 cells in each of two planes although 4 in one plane is not rare. The presence of a micro-grain or micro-cell, a small, extra cell within the tetrad wall, was occasionally noted.

Apparently normal groups:	
1. Two cells in each of two planes	417
2. Four cells in one plane	72
Apparently abnormal groups:	
1. Two cells in two planes plus one micro-grain	28
2. Four cells in one plane plus one micro-grain	4
3. Two cells in one plane (diad) plus one micro-grain	1
4. Three cells in one plane (triad) plus one micro-grain	5
TOTAL	527

Of tetrads examined 7.2 per cent showed irregularities.

Pollen.—In general the pollen grains range from elliptical to spherical. Of 500 grains examined 54 (10.8 per cent) were empty and some of them were distorted. (See pl. 33). Four of the empty grains were about one-third the normal size. The full regular cells are slightly larger than those of *P. callosum* and *P. Lawrenceanum*.

Measurements of 100 *Maudiae* pollen grains and 100 each of *callosum* and *Lawrenceanum* indicated that those of *Maudiae* average .0580 mm. along the long axis, while those of *callosum* and *Lawrenceanum* are .0530 and .0526 respectively. That the slight difference in size between the grains of the offspring and the parents is not merely based on variation within the samples was confirmed with a standard deviation test.

In both species and in the hybrid, leptotene and zygotene probably occur when the bud is quite small. Just how soon pachytene begins is not known but apparently pachytene and pachytene-early diplotene go on for considerable time, sometimes even a matter of days, depending upon environmental conditions. The remaining stages, particularly diakinesis and metaphase I, progress rapidly.

The lengths of some buds, divested of enfolding bracts, are listed together with the meiotic stages exhibited:

P. callosum

13.0 mm.....Pachytene

15.0 mm.....Pachytene

16.5 mm.....Pachytene to diakinesis; Early metaphase I; Metaphase I

17.0 mm.....Primarily diads. A few metaphase and anaphase I cells

18.0 mm.....Tetrads

P. Lawrenceanum

16.5 mm.....Pachytene, early diplotene

18.0 mm.....A few metaphase and anaphase I cells but chiefly division 2; Division 2; Tetrads

18.5 mm.....Division 2

19.0 mm.....Pollen grains

× *P. Maudiae*

13.0 mm.....Pachytene

15.5 mm.....Pachytene

16.5 mm.....Diakinesis to early metaphase I

17.0 mm.....Pachytene; Pachytene to diakinesis; Pachytene to mid-metaphase I

18.0 mm.....1. Metaphase I
2. Telephase I through division 2

18.5 mm.....Tetrads

V. Discussion

It will be noticed in the anaphase I data of the hybrid that of the 49 cells listed as showing disorders, group *c* (13 cells) is characterized by one bridge and one fragment. This is the typical result of pairing between two chromosomes when one of them has an inversion not involving the centromere and a crossover occurs within the inverted region.

Group *a* (17 cells) exhibits the bridge but no fragment. Two possibilities exist here: either the fragment was not visible or it did not exist. Since none of the fragments observed either with or without bridges were large it is possible that in these cases it had been displaced by smearing or that it had been concealed by

the chromosomes at one or the other of the poles. There being evidence that inversions exist, this possibility must be given the more credence. The other possibility is that in these cells no fragment existed as a result of an inversion bridge. This would necessitate another hypothesis for the origin of a bridge without a fragment, and there is no evidence here to support such a hypothesis. The single cell in group *b* with two bridges but no fragments should be considered in the same light except that in this group two chromosome pairs were probably involved.

Group *e* (2 cells) is characterized by two bridges and one fragment. The most logical assumption here is that one of the fragments was rendered invisible as in the case above. The single instance of one bridge and two fragments *(d)* may well indicate the breakage of one bridge before the other. In these cases, as in *b*, two chromosome pairs would be involved.

Group *f* is composed of 15 cells which showed one fragment or small isolated chromosome. It is thought that these were true fragments since they were quite small. In such a case the bridge would have been already broken. However, the possibility that these might have been lagging chromosomes cannot be overlooked since many of the typical mid-metaphase I bivalents of the hybrid are small.

An interesting case is presented by the pair of chromosomes of intermediate length with prominent secondary constriction. It is this pair which exhibits the inversion mentioned in the section on root-tip analysis. (See pl. 32). Half of the chromosome is involved in the inversion for which the hybrid examined is heterozygous, and the inversion, when viewed under the microscope, appears to be terminal. The possibility must not be overlooked that there is chromatin material here which cannot be seen and would render the inversion interstitial. It has long been felt that inversions generally did not involve chromosome ends (Darlington, 1937; Kossikov & Muller, 1935; Muller, 1938). However, there is considerable evidence to date that terminal inversions do occur (Kauffmann, 1937; Sutton, 1940; Carson, 1944; Carson & Stalker, 1947), and the possibility that the inversion mentioned here is truly terminal must not be brushed aside. This inversion, since it involves the centromere, would not bring about the formation of a bridge. A single crossover within the inversion would result in a duplication-deficiency chromatid as well as one complete chromatid going to each pole. Of the complete chromatids, one would show the inversion (Sturtevant & Beadle, 1939).

It will be noticed that although 10.1 per cent of the anaphase I cells exhibited disorders, only 7.2 per cent of the hybrid tetrads were visibly abnormal. This probably can be taken to mean that some of the tetrads, although appearing normal, are not so. It cannot be said that there is any absolute correlation between the 10.8 per cent visibly non-viable pollen and the similar percentage of visible anaphase I abnormalities even though it is suggestive. No doubt there are other factors to be considered. The 10.8 per cent of non-staining pollen grains is not a true estimate of the hybrid's sterility in view of growers' experiences in attempting to use *Maudiae* as a parent plant. There are, no doubt, many pollen grains which appear quite normal but whose viability is terminated at later stages. Male gametes

may become non-viable in the pollen tube; the pollen tube may grow too slowly; the egg may be non-viable; the zygote may be non-viable; or the seedling perish early in its existence.

That the 10.8 per cent non-viable pollen is not a complete picture of the sterility of the hybrid is supported by what is known of pairing in *Maudiae*. It will be remembered that pairing in *Maudiae* was typically indicated by 17 bivalents at metaphase I. This suggests pairing between two *Lawrenceanum* chromosomes, and if two chromosomes are like enough to pair consistently this would in turn suggest polyploidy. It is entirely reasonable to assume that such pairing is the result of polyploidy. A glance at the list of chromosome numbers at the close of section III reveals that throughout subgenera BRACHYPETALUM and ANATOPEDILUM the *n* number is 13. In the subgenus OTOPEDILUM, the group to which all of the individuals dealt with in this study belong, higher *n* numbers approach the triploid level. It is suggested that this increase in chromosome number is the result of hybridization between groups that cannot be named at this time for lack of evidence.

The mere statement that pairing in *Maudiae* is in 17 bivalents and that the 2 remaining *Lawrenceanum* chromosomes pair is probably an over-simplification. *P. callosum* is characterized, as we have seen, by a chromosome set of 6 pairs of terminal or subterminal chromosomes and 10 interstitial pairs while *P. Lawrenceanum* possesses 10 terminal or subterminal pairs and 8 interstitial pairs. The difficulties of pairing a *Lawrenceanum* and a *callosum* chromosome for each of 16 bivalents (in addition to the bivalent already formed by each of two *Lawrenceanum* chromosomes), in view of the differences in morphology, are apparent. It is highly probable that some *callosum* chromosomes are pairing amongst themselves as well as with *Lawrenceanum* chromosomes, and this possibility would exist equally well for chromosomes of *Lawrenceanum*. Under such conditions gametes could be produced which would lack necessary genic elements. From the foregoing facts it seems logical to conclude that the causes of sterility in the hybrid are:

1. Visible disorders in anaphase I due to inversions.

2. Invisible disorders at anaphase I due to an inversion which includes the centromere and therefore results in duplication-deficiencies.

3. Pairing of some *callosum* chromosomes and some of the *Lawrenceanum* chromosomes among themselves (because of their polyploid background) takes place so that some of the gametes are without necessary chromatin material.

VI. SUMMARY

1. A cytological study was made of the × *Paphiopedilum Maudiae* Hort., the result of a cross between the albino forms of *P. callosum* and *P. Lawrenceanum*. Because of its high sterility, *P. Maudiae* as a parent plant has rarely, if ever, produced any offspring of a quality equal to, or exceeding, its own.

2. A short discussion of the genus and the histories of the parental forms and the offspring are set forth.

3. Some observations are made on the status of × *Paphiopedilum Maudiae* Hort. as a parent plant.

4. A cytological analysis of root-tips of the parental forms and the hybrid gave the following results:

a. Chromosome numbers of *P. callosum*, *P. Lawrenceanum*, and *P. Maudiae* are confirmed as being 32, 36, and 34, respectively. Two other species counts were also confirmed (*P. barbatum*, 38; *P. Curtissii*, 36; *P. superbiens*, 38).

b. *P. callosum* has 6 pairs of chromosomes with terminal or subterminal centromeres and 10 pairs with interstitial centromeres.

c. *P. Lawrenceanum* has 8 pairs with interstitial centromeres and 10 with terminal or subterminal centromeres.

d. *P. Maudiae* is heterozygous for an inversion which seems to be terminal.

5. Study of meiosis in the parental forms and the hybrid gave the following results:

a. *P. callosum* and *P. Lawrenceanum* undergo normal meioses with bivalent pairing.

b. Pairing in *P. Maudiae* is in 17 bivalents. Some disorders are visible at anaphase I.

c. Only 10.8 per cent of the *Maudiae* pollen grains are visibly nonviable. This does not give a true picture of the sterility of the plant.

6. Some conclusions are offered as to the several causes of sterility of the hybrid:

a. Inversions that give rise to anaphase I disorders.

b. An inversion, visibly terminal upon microscopic examination, which does not give rise to visible anaphase I disorders because it includes the centromere.

c. As a result of polyploidy in the genus some of the *callosum* chromosomes pair with themselves as do some of the *Lawrenceanum* chromosomes in meiosis of hybrid pollen mother cells. Some of the gametes are therefore deprived of necessary chromatin material.

Literature Cited

Anon. (1912). *Cypripedium callosum Sanderae*. Jour. Hort. **65**:565.
Black, J. M. (1933). Albinism in Cypripediums. Orchid Rev. **41**:69–72.
Buser, R. (1894). *Cypripedium* ou *Cypripedilum*? Bull. Herb. Boiss. **2**:642–644.
Carson, H. L. (1944). An analysis of natural chromosome variability in *Sciara impatiens* Johannsen. Jour. Morph. **75**:11–59.
———, and Stalker, H. D. (1947). Gene arrangements in natural populations of *Drosophila robusta* Sturtevant. Evolution **1**:113–133.
Cooper, E. (1946). White Cypripediums. Orchid Rev. **54**:106–107.
Darlington, C. D. (1937). Recent Advances in Cytology, 2nd ed. Philadelphia.
Duncan, R. E. (1945). Production of variable aneuploid numbers of chromosomes within the root tips of *Paphiopedilum Wardii*. Am. Jour. Bot. **32**:506–509.
———, (1947). The hybrid Lady Slipper. Orchid Dig. **11**:199–207.
———, and MacLeod, R. A. (1948a). Chromosomes of the Brachypetalums. Am. Orchid Soc. Bull. **17**:170–174.

———, ———, (1948b). Chromosomes of the *insigne* complex of ladyslippers. *Ibid.* 424–429.
———, ———, (1949a). The chromosomes of the continental species of *Paphiopedilum* with solid green leaves. *Ibid.* **18**:84–89.
———, ———, (1949b). The chromosomes of some of the Polyantha. *Ibid.* 159–163.
Francini, E. (1931). Ricerche embriologiche e cariologiche sul genere "Cypripedium". Nuovo Giorn. Bot. Ital. N. S. **38**:154–212.
———, (1932). Un reperto cariologico nella F_2 di "× *Paphiopedilum Leeanum*". *Ibid.* **39**:251–253.
———, (1934). Ibridazione interspecifica nel genere "Paphiopedilum." *Ibid.* **41**:189–237.
Hooker, J. D. (1879). *Cypripedium Laurenceanum.* Curtis's Bot. Mag. *tab. 632.*
Kauffmann, B. P. (1936). A terminal inversion in *Drosophila ananassae.* Proc. Nat. Acad. Sci. **22**:591–594.
Kossikov, R. V., and Muller, H. J. (1933). Invalidation of the genetic evidence for branched chromonenas. Jour. Hered. **26**:305–317.
Mehlquist, G. A. L. (1947a). Polyploidy in the genus *Paphiopedilum* Pfitz. (*Cypripedium* Hort.), and its practical implications. Mo. Bot. Gard. Bull. **35**:211–225
———, (1947b). Some smear techniques for counting chromosomes in orchids. *Ibid.* 229–233.
Meyer, J. R. (1943). Colchicine-Feulgen leaf smears. Stain Technol. **18**:53–56.
Muller, H. J. (1938). The remaking of chromosomes. Collecting Net **13**, No. 8.
Pfitzer, E. (1903). Orchidaceae–Pleonandrae. Engler's Das Pflanzenreich, IV, Fam. 50 (Heft 12).
Reichenbach, H. G. (1854). Xenia Orchidacea **3**.
———, (1878). *Cypripedium Lawrenceanum.* Gard. Chron. II, **18**:748.
———, (1885). Lindenia **1**:89, *pl. 42.*
———, (1886). *Cypripedium callosum,* n. sp. Gard. Chron. II, **26**:326.
Rolfe, R. A. (1896). The Cypripedium group. Orchid Rev. **4**:327–334; 363–367.
[———,] (1900). *Cypripedium* × *Maudiae. Ibid.* 8:308.
Sander, C. F., F. K., and L. L. (1927). Sander's Orchid Guide. Rev. ed. Antwerp.
Sander, F. K. (1946). Sander's Complete List of Orchid Hybrids. St. Albans.
Stockwell, P. A. (1934). A stain for difficult plant material. Science N. S. **80**:121–122.
Sturtevant, A. H., and Beadle, G. W. (1939). An Introduction to Genetics. Philadelphia and London.
Sutton, E. (1940). Terminal deficiencies in the × chromosome of *Drosophila Melanogaster.* Genetics **25**:534–540.
[Wilson, Gurney], (1933). *Cypripedium Maudiae.* Orchid Rev. **31**:299–300.

CHART I

A LIST OF THE CROSSES IN WHICH P. MAUDIAE HAS BEEN USED AS A PARENT.

THE NUMBERS BELOW EACH VARIETAL NAME INDICATE HOW MANY TIMES THE VARIETY HAS BEEN USED AS A PARENT.
TO THE RIGHT OF THE ANTECEDENT SPECIES ARE THE SECTIONS OF OTOPEDILUM OR THE SUBGENERA TO WHICH THEY BELONG.

MAUDIAE (SECTION PHACOPETALUM OF SUBGENUS OTOPEDILUM)
35

1. X ACTAEUS = MAUD GREEN. ACTAEUS
84 — 0
- INSIGNE — NEUROPETALUM
- LEEANUM
  - INSIGNE — NEUROPETALUM
  - SPICERIANUM — CYMATOPETALUM

2. X ALMA GAVAERT = ALMAUD. ALMA GAVAERT
11 — 0
- MAUDIAE
  - CALLOSUM VAR. SANDERAE — PHACOPETALUM
  - LAWRENCEANUM VAR. HYEANUM — PHACOPETALUM
- LAWRENCEANUM VAR. HYEANUM — PHACOPETALUM

3. X ARMISTICE II = ARMAMENT ARMISTICE II
12 — 0
- ANTINOUS
  - ACTAEUS
    - INSIGNE — NEUROPETALUM
    - LEEANUM
      - INSIGNE — NEUROPETALUM
      - SPICERIANUM — CYMATOPETALUM
  - J. HOWE – ?
- NITENS
  - INSIGNE — NEUROPETALUM
  - VILLOSUM — NEUROPETALUM

4. X AUREUM = BENITA. AUREUM
58 — 0
- NITENS
  - INSIGNE — NEUROPETALUM
  - VILLOSUM — NEUROPETALUM
- SPICERIANUM — CYMATOPETALUM

5. X BINGLEYENSE = COLOURFUL. BINGLEYENSE
21 — 0
- CHARLESWORTHII — NEUROPETALUM
- HARRISIANUM
  - BARBATUM — PHACOPETALUM
  - VILLOSUM — NEUROPETALUM

6. X CALLOSO-BARBATUM = METEORITE. CALLOSO-BARBATUM
10 — 0
- CALLOSUM — PHACOPETALUM
- BARBATUM — PHACOPETALUM

7. X CALLOSUM = HOLDENII CALLOSUM (J.P.) — PHACOPETALUM
55 — 6

8. X CHAMBERLAINIANUM = IRIS II. CHAMBERLAINIANUM (J.P.) — COCHLOPETALUM
30 — 0

9. X CILIOLARE = COLORADO CILIOLARE (J.P.) — PHACOPETALUM
27 — 0

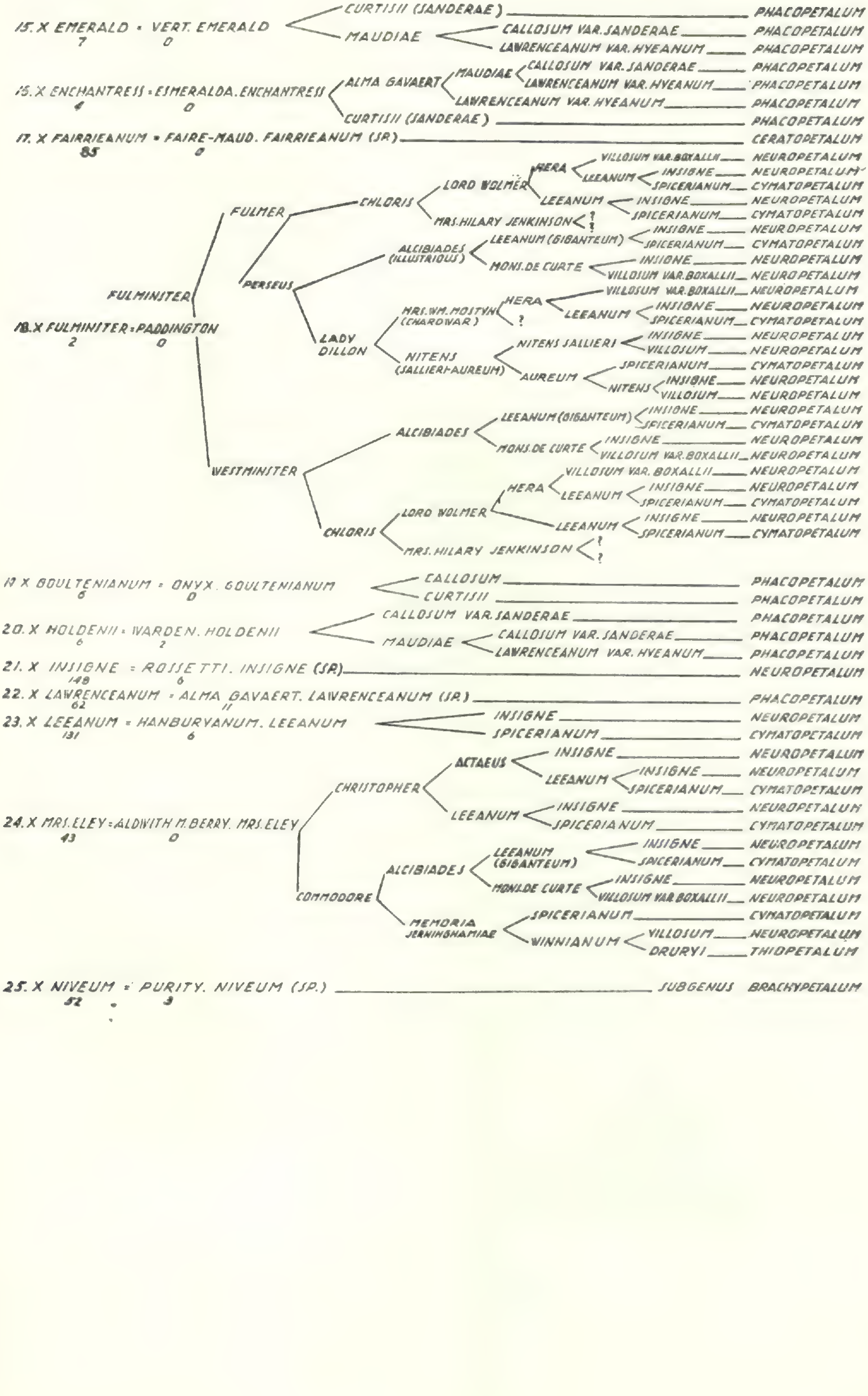
10. X CLAIRE DE LUNE = MITYLENE. CLAIRE DE LUNE
2 — 0
- EMERALD
  - CURTISII (SANDERAE) — PHACOPETALUM
  - MAUDIAE
    - CALLOSUM VAR. SANDERAE — PHACOPETALUM
    - LAWRENCEANUM VAR. HYEANUM — PHACOPETALUM
- ALMA GAVAERT
  - MAUDIAE
    - CALLOSUM VAR. SANDERAE — PHACOPETALUM
    - LAWRENCEANUM VAR. HYEANUM — PHACOPETALUM
  - LAWRENCEANUM VAR. HYEANUM — PHACOPETALUM

11. X CRUSADER = PALESTINE. CRUSADER
8 — 0
- JULIAN
  - AUREUM (OEDIPPE)
    - NITENS SALLIERI HYEANUM
      - INSIGNE — NEUROPETALUM
      - VILLOSUM — NEUROPETALUM
    - SPICERIANUM MAGNIFICUM — CYMATOPETALUM
  - VAN DYCK
    - HIRSUTISSIMUM HYBRID — STICTOPETALUM
    - MONS. DE CURTE
      - INSIGNE — NEUROPETALUM
      - VILLOSUM VAR. BOXALLII — NEUROPETALUM
- LUCIFER
  - HERA (EURYADES)
    - VILLOSUM VAR. BOXALLII — NEUROPETALUM
    - LEEANUM
      - INSIGNE — NEUROPETALUM
      - SPICERIANUM — CYMATOPETALUM
  - NIOBE
    - SPICERIANUM — CYMATOPETALUM
    - FAIRRIEANUM — CERATOPETALUM

12. X CURTISII = EMERALD. CURTISII (J.P.)
44 — 7
— PHACOPETALUM

13. X DORA = MAUDORA. DORA
5 — 0
- ACTAEUS
  - INSIGNE — NEUROPETALUM
  - LEEANUM
    - INSIGNE — NEUROPETALUM
    - SPICERIANUM — CYMATOPETALUM
- ILLUSTRE
  - LATHAMIANUM
    - SPICERIANUM — CYMATOPETALUM
    - VILLOSUM — NEUROPETALUM
  - NITENS (SANDER'S)
    - INSIGNE — NEUROPETALUM
    - VILLOSUM — NEUROPETALUM

14. X EARL OF CHESTER = SUNSET. EARL OF CHESTER
6 — 0
- BINGLEYENSE (CHORLTONII)
  - CHARLESWORTHII — NEUROPETALUM
  - HARRISIANUM
    - BARBATUM — PHACOPETALUM
    - VILLOSUM — NEUROPETALUM
- LORD ROBERTS
  - CHARLESWORTHII — NEUROPETALUM
  - CREON
    - HARRISIANUM
      - BARBATUM — PHACOPETALUM
      - VILLOSUM — NEUROPETALUM
    - CENANTHUM ?


15. X EMERALD • VERT. EMERALD
7 0
CURTISII (SANDERAE) PHACOPETALUM
MAUDIAE
CALLOSUM VAR. SANDERAE PHACOPETALUM
LAWRENCEANUM VAR. HYEANUM PHACOPETALUM
16. X ENCHANTRESS • ESMERALDA. ENCHANTRESS
4 0
ALMA GAVAERT
MAUDIAE
CALLOSUM VAR. SANDERAE PHACOPETALUM
LAWRENCEANUM VAR. HYEANUM PHACOPETALUM
LAWRENCEANUM VAR. HYEANUM PHACOPETALUM
CURTISII (SANDERAE) PHACOPETALUM
17. X FAIRRIEANUM • FAIRE-MAUD. FAIRRIEANUM (SR.) CERATOPETALUM
85 0
18. X FULMINITER • PADDINGTON
2 0
FULMINITER
FULMER
CHLORIS
LORD WOLMER
HERA
VILLOSUM VAR. BOXALLII NEUROPETALUM
LEEANUM
INSIGNE NEUROPETALUM
SPICERIANUM CYMATOPETALUM
LEEANUM
INSIGNE NEUROPETALUM
SPICERIANUM CYMATOPETALUM
MRS. HILARY JENKINSON ? ?
PERSEUS
ALCIBIADES (ILLUSTRIOUS)
LEEANUM (GIGANTEUM)
INSIGNE NEUROPETALUM
SPICERIANUM CYMATOPETALUM
MONS. DE CURTE
INSIGNE NEUROPETALUM
VILLOSUM VAR. BOXALLII NEUROPETALUM
LADY DILLON
MRS. WM. MOSTYN (CHAROVAR)
HERA
VILLOSUM VAR. BOXALLII NEUROPETALUM
LEEANUM
INSIGNE NEUROPETALUM
SPICERIANUM CYMATOPETALUM
?
NITENS (SALLIERI-AUREUM)
NITENS SALLIERI
INSIGNE NEUROPETALUM
VILLOSUM NEUROPETALUM
AUREUM
SPICERIANUM CYMATOPETALUM
NITENS
INSIGNE NEUROPETALUM
VILLOSUM NEUROPETALUM
WESTMINSTER
ALCIBIADES
LEEANUM (GIGANTEUM)
INSIGNE NEUROPETALUM
SPICERIANUM CYMATOPETALUM
MONS. DE CURTE
INSIGNE NEUROPETALUM
VILLOSUM VAR. BOXALLII NEUROPETALUM
CHLORIS
LORD WOLMER
HERA
VILLOSUM VAR. BOXALLII NEUROPETALUM
LEEANUM
INSIGNE NEUROPETALUM
SPICERIANUM CYMATOPETALUM
LEEANUM
INSIGNE NEUROPETALUM
SPICERIANUM CYMATOPETALUM
MRS. HILARY JENKINSON ? ?
19. X BOULTENIANUM • ONYX. BOULTENIANUM
6 0
CALLOSUM PHACOPETALUM
CURTISII PHACOPETALUM
20. X HOLDENII • WARDEN. HOLDENII
6 2
CALLOSUM VAR. SANDERAE PHACOPETALUM
MAUDIAE
CALLOSUM VAR. SANDERAE PHACOPETALUM
LAWRENCEANUM VAR. HYEANUM PHACOPETALUM
21. X INSIGNE • ROSSETTI. INSIGNE (SP.) NEUROPETALUM
148 6
22. X LAWRENCEANUM • ALMA GAVAERT. LAWRENCEANUM (SP.) PHACOPETALUM
62 11
23. X LEEANUM • HANBURYANUM. LEEANUM
131 6
INSIGNE NEUROPETALUM
SPICERIANUM CYMATOPETALUM
24. X MRS. ELEY • ALDWITH M. BERRY. MRS. ELEY
43 0
CHRISTOPHER
ACTAEUS
INSIGNE NEUROPETALUM
LEEANUM
INSIGNE NEUROPETALUM
SPICERIANUM CYMATOPETALUM
LEEANUM
INSIGNE NEUROPETALUM
SPICERIANUM CYMATOPETALUM
COMMODORE
ALCIBIADES
LEEANUM (GIGANTEUM)
INSIGNE NEUROPETALUM
SPICERIANUM CYMATOPETALUM
MONS. DE CURTE
INSIGNE NEUROPETALUM
VILLOSUM VAR. BOXALLII NEUROPETALUM
MEMORIA JERNINGHAMIAE
SPICERIANUM CYMATOPETALUM
WINNIANUM
VILLOSUM NEUROPETALUM
DRURYI THIOPETALUM
25. X NIVEUM • PURITY. NIVEUM (SP.) SUBGENUS BRACHYPETALUM
52 3

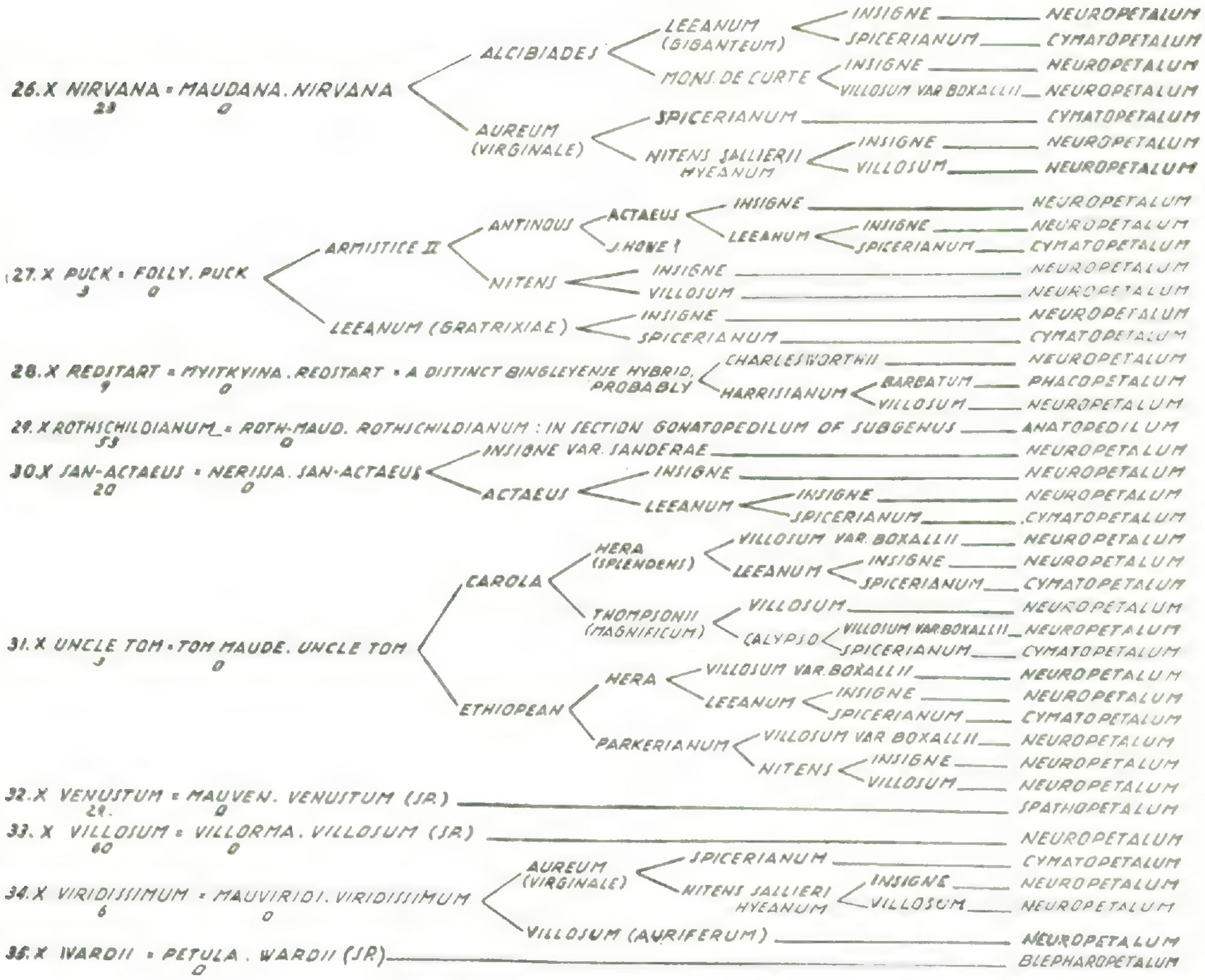

26. X NIRVANA = MAUDANA. NIRVANA
23 0
ALCIBIADES
LEEANUM (GIGANTEUM)
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
MONS. DE CURTE
INSIGNE — NEUROPETALUM
VILLOSUM VAR BOXALLII — NEUROPETALUM
AUREUM (VIRGINALE)
SPICERIANUM — CYMATOPETALUM
NITENS SALLIERII HYEANUM
INSIGNE — NEUROPETALUM
VILLOSUM — NEUROPETALUM
27. X PUCK = FOLLY. PUCK
3 0
ARMISTICE II
ANTINOUS
ACTAEUS
INSIGNE — NEUROPETALUM
LEEANUM
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
J. HOWE ?
NITENS
INSIGNE — NEUROPETALUM
VILLOSUM — NEUROPETALUM
LEEANUM (GRATRIXIAE)
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
28. X REDSTART = MYITKYINA. REDSTART = A DISTINCT BINGLEYENSE HYBRID, PROBABLY
CHARLESWORTHII — NEUROPETALUM
HARRISIANUM
BARBATUM — PHACOPETALUM
VILLOSUM — NEUROPETALUM
29. X ROTHSCHILDIANUM = ROTH-MAUD. ROTHSCHILDIANUM : IN SECTION GONATOPEDILUM OF SUBGENUS — ANATOPEDILUM
55 0
30. X SAN-ACTAEUS = NERISSA. SAN-ACTAEUS
20 0
INSIGNE VAR. SANDERAE — NEUROPETALUM
ACTAEUS
INSIGNE — NEUROPETALUM
LEEANUM
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
31. X UNCLE TOM = TOM MAUDE. UNCLE TOM
3 0
CAROLA
HERA (SPLENDENS)
VILLOSUM VAR. BOXALLII — NEUROPETALUM
LEEANUM
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
THOMPSONII (MAGNIFICUM)
VILLOSUM — NEUROPETALUM
CALYPSO
VILLOSUM VAR. BOXALLII — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
ETHIOPEAN
HERA
VILLOSUM VAR. BOXALLII — NEUROPETALUM
LEEANUM
INSIGNE — NEUROPETALUM
SPICERIANUM — CYMATOPETALUM
PARKERIANUM
VILLOSUM VAR BOXALLII — NEUROPETALUM
NITENS
INSIGNE — NEUROPETALUM
VILLOSUM — NEUROPETALUM
32. X VENUSTUM = MAUVEN. VENUSTUM (JR.)
29. 0
— SPATHOPETALUM
33. X VILLOSUM = VILLORMA. VILLOSUM (JR.)
60 0
— NEUROPETALUM
34. X VIRIDISSIMUM = MAUVIRIDI. VIRIDISSIMUM
6 0
AUREUM (VIRGINALE)
SPICERIANUM — CYMATOPETALUM
NITENS JALLIERI HYEANUM
INSIGNE — NEUROPETALUM
VILLOSUM — NEUROPETALUM
VILLOSUM (AURIFERUM) — NEUROPETALUM
35. X WARDII = PETULA. WARDII (JR.)
0
— BLEPHAROPETALUM

CHART II

LIST OF CROSSES IN WHICH *P. CALLOSUM* HAS BEEN USED AS A PARENT

Section of OTOPEDILUM (or other subgenera) used in cross		Species or hybrid used as parent*		Resulting progeny	
1. PHACOPETALUM	×	ALMA GAVAERT (Chart I #2)†	11‡	NEREID	0‡
2. PHACOPETALUM NEUROPETALUM	×	APPLETONIANUM (App. Chart. II #1)	4	SIAMENSE	1
3. PHACOPETALUM	×	*Argus*	40	CALLOSO-ARGUS	0
4. PHACOPETALUM NEUROPETALUM	×	ASHBURTONIAE (App. Chart II #2)	12	ZENOBIA	1
5. NEUROPETALUM CYMATOPETALUM	×	AUREUM (Chart I #11)	58	ALTRICHAMENSE	0
6. PHACOPETALUM	×	*barbatum*	49	CALLOSO-BARBATUM	10
7. Subg. BRACHYPETALUM	×	*bellatulum*	57	WOTTONII	1
8. NEUROPETALUM	×	*Boxallii* (var. of sp. *villosum*)§	42	J. BARTELS	0
9. PHACOPETALUM Subg. ANATOPEDILUM Sect. CORYOPEDILUM	×	CALLO-ROTHSCHILDIANUM (App. Chart II #3)	1	FRANCONIA	0
10. PHACOPETALUM SPATHOPETALUM	×	CALOPHYLLUM (App. Chart II, #4)	13	PALLAS	2
11. COCHLOPETALUM	×	*Chamberlainianum*	38	ALCIPPE	0
12. NEUROPETALUM	×	*Charlesworthii*	66	ROSITA	0
13. PHACOPETALUM	×	*ciliolare*	27	ZEUS	0
14. Subg. BRACHYPETALUM	×	*concolor*	27	CONCO-CALLOSUS	0
15. PHACOPETALUM	×	*Curtisii*	44	GOULTENIANUM	6
16. Subg. BRACHYPETALUM	×	*Delenatii*	14	MME. MARTINET	1
17. THIOPETALUM	×	*Druryi*	33	A. R. SMITH	0
18. NEUROPETALUM	×	*exul*	20	DR. CONWAY	0
19. CERATOPETALUM	×	*Fairrieanum*	85	JUNO	1
20. PHACOPETALUM NEUROPETALUM	×	*gigas* (App. Chart II, #5)	8	E. J. SEYMOUR	0
21. Subg. BRACHYPETALUM	×	*Godefroyae*	31	FELIX FAURE	0
22. PHACOPETALUM	×	GOULTENIANUM (Chart II, #15)	6	MALHERBE	0
23. PHACOPETALUM	×	GOWERIANUM (App. to Chart II, #6)	19	HORTENSE	0
24. PHACOPETALUM NEUROPETALUM	×	HARRISIANUM (App. to Chart II, #1)	72	LEDOUXIAE	1
25. STICTOPETALUM	×	*hirsutissimum*	33	DONCASTERIANUM	0
26. NEUROPETALUM	×	HITCHINSIAE (App. to Chart II, #7)	17	SONIA	0
27. PHACOPETALUM	×	HOLDENII (Chart II, #37)	6	GLORIOSUM	0
28. SPATHOPETALUM	×	*Hookerae*	26	FORTUNA	0
29. NEUROPETALUM	×	*insigne*	148	LEONIAE	2
30. BLEPHAROPETALUM	×	*javanicum*	7	JAVA	0

*Species names are indicated in italics; hybrids, subgenera, and sections in caps.
†Key to explanations of varietal backgrounds are given in parentheses.
‡The figures following the names indicate the number of times the plant has been used in crosses.
§Treated as *P. villosum* var. *Boxallii* in Sander's 'Complete List of Orchid Hybrids'; treated as species *P. Boxallii* by G. A. L. Mehlquist (1947) and R. E. Duncan (1947).

Section of Otopedilum (or other subgenera) used in cross		Species or hybrid used as parent*		Resulting progeny	
31. Neuropetalum Cymatopetalum Subg. Brachypetalum	×	J. M. Black (App. Chart II, #8)	46	James	0
32. Cymatopetalum Neuropetalum	×	Lathamianum (App. Chart II, #9)	39	Calliope	0
33. Phacopetalum	×	*Lawrenceanum*	62	Maudiae	35
34. Neuropetalum Cymatopetalum	×	Leeanum (Chart I, #1)	132	Angeliae	0
35. ?	×	Madame Coffinet	2	Madam Maxine Opoix	0
36. Blepharopetalum	×	*Mastersianum*	24	Pytho	0
37. Phacopetalum	×	Maudiae (Chart I, #2)	35	Holdenii	6
38. Neuropetalum	×	nitens (Chart I, #3)	66	Wendigo	0
39. Subg. Brachypetalum	×	*niveum*	48	Winifred Hollington	1
40. Phacopetalum Neuropetalum	×	oenanthum (App. Chart III, #2)	28	Olga Bogshawe	0
41. Subg. Anatopedilum Sect. Coryopedilum	×	*phillippinense*	22	Millmanii	0
42. Subg. Anatopedilum Sect. Coryopedilum	×	*Rothschildianum*	53	callo-Roths-childianum	1
43. Subg. Anatopedilum Sect. Coryopedilum	×	*Sanderianum*	13	Princess May	0
44. Blepharopetalum	×	sementa (App. Chart II, #10)	8	Aurelianense	0
45. Cymatopetalum	×	*Spicerianum*	62	Mlle. Gabrielle Moens	0
46. Subg. Anatopedilum Sect. Prenipedilum	×	*Stonei*	27	Fordianum	0
47. Phacopetalum	×	*superbiens*	39	Moussetianum	0
48. Phacopetalum	×	superciliare (App. Chart II, #11)	18	Moreauanum	0
49. Phacopetalum Subg. Brachypetalum	×	Tautzianum (App. Chart II, #12)	2	Nandii	0
50. Blepharopetalum	×	*tonsum*	33	Felicity	0
51. Phacopetalum Neuropetalum	×	triumphans (App. Chart II, #13)	1	Rajah	0
52. Spathopetalum	×	*venustum*	29	Orpheus	3
53. Neuropetalum	×	*villosum*	60	Indra	0
54. Phacopetalum Blepharopetalum	×	William Matthews (App. Chart II, #14)	1	Ernest Read	2
55. Phacopetalum Subg. Brachypetalum	×	Winifred Hollington (App. Chart II, #15)	1	Winsum	0
					74

APPENDIX TO CHART II

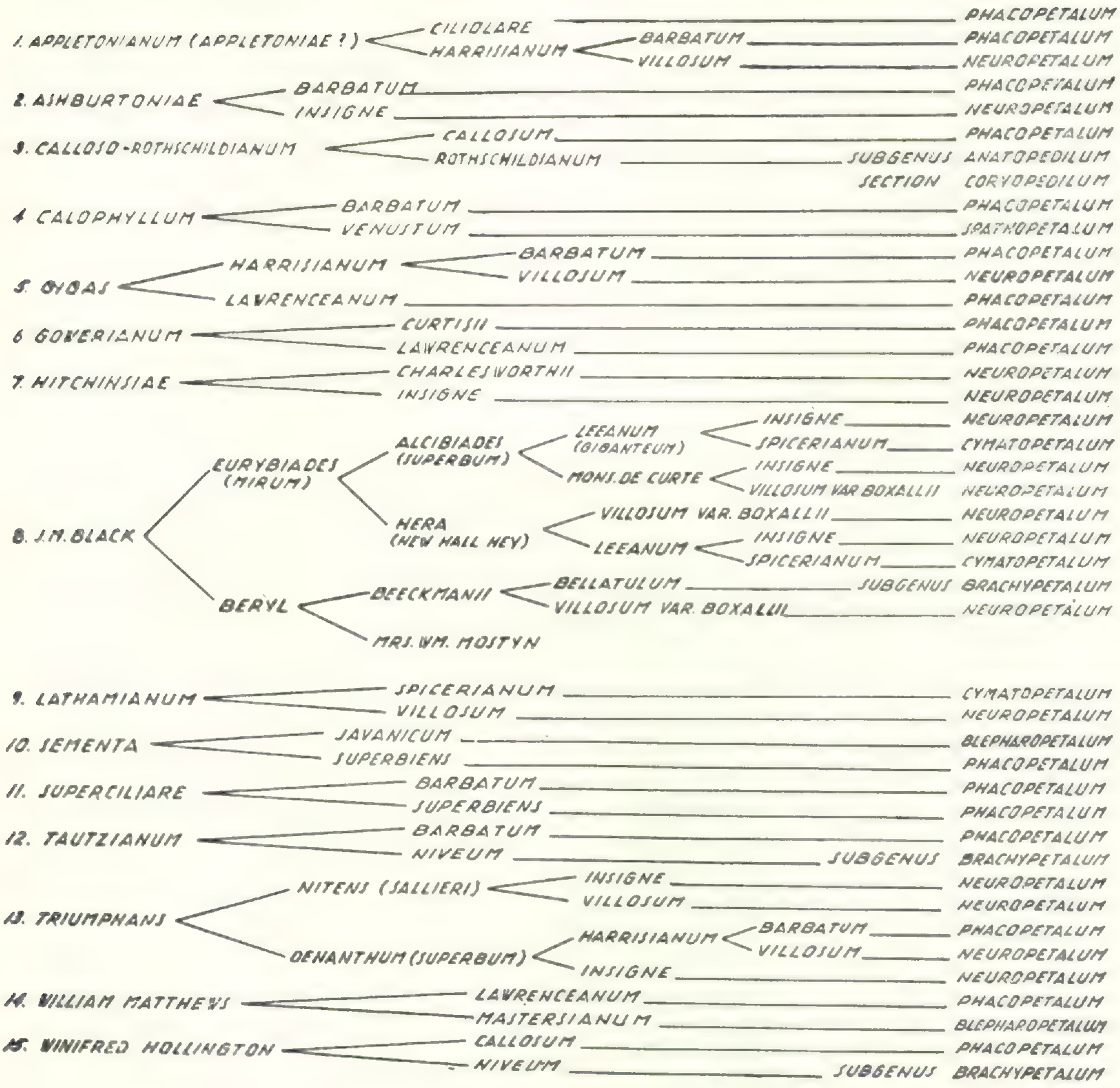


CHART III

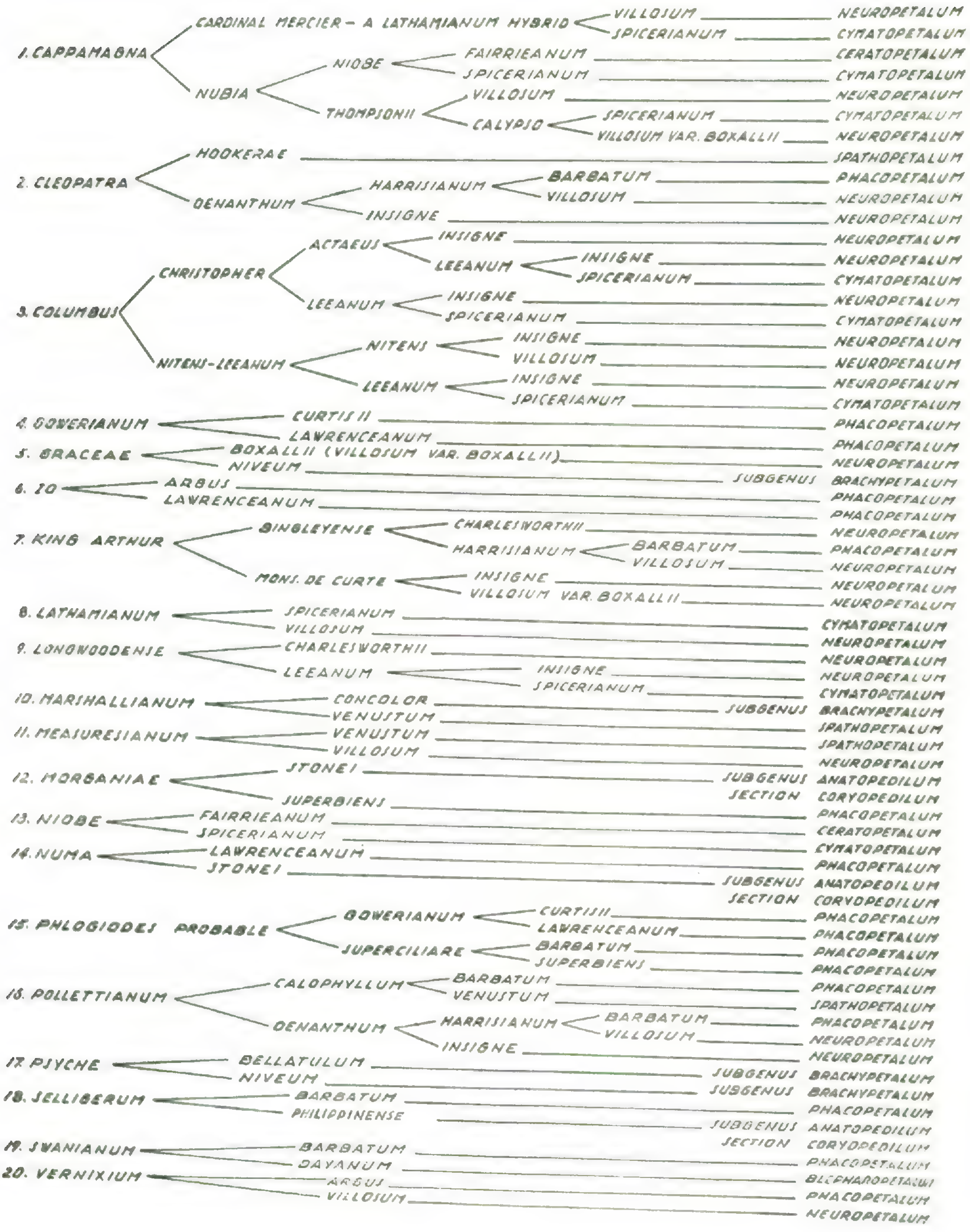
LIST OF CROSSES IN WHICH *P. LAWRENCEANUM* HAS BEEN USED AS A PARENT*

Section of Otopedilum (or other subgenera) used in cross		Species or hybrid used as parent		Resulting progeny	
1. Phacopetalum	×	Alma Gavaert (Chart I, #2)	11	Eleanor Rozilla	0
2. Phacopetalum	×	*Argus*	40	Io	15
3. Phacopetalum	×	*barbatum*	49	Almum	3
4. Subg. Brachypetalum	×	*bellatutum*	57	Laure-Bel	2
5. Neuropetalum	×	*villosum* var. *Boxallii*	42	Thayerianum	0
6. Phacopetalum	×	calloso-barbatum (Chart I, #6)	10	Myth	0
7. Phacopetalum	×	*callosum*	55	Maudiae	35
8. Neuropetalum Cymatopetalum Ceratopetalum	×	cappamagna (App. to Chart III, #1)	46	Montrose	0
9. Cochlopetalum	×	*Chamberlainianum*	38	Hiero	0
10. Neuropetalum	×	*Charlesworthii*	66	decipiens	0
11. Phacopetalum	×	*ciliolare*	27	Smithii	4
12. Spathopetalum Phacopetalum Neuropetalum	×	Cleopatra (App. to Chart III, #2)	1	resplendens	0
13. Neuropetalum Cymatopetalum	×	Columbus (App. to Chart II, #3)	11	Sardow	0
14. Subg. Brachypetalum	×	*concolor*	27	Conco-Laure	0
15. Phacopetalum	×	*Curtisii*	44	Gowerianum	19
16. Blepharopetalum	×	*Dayanum*	26	Littleanum	0
17. Thiopetalum	×	*Druryi*	33	Cybele	0
18. Neuropetalum	×	*exul*	20	Julia	0
19. Ceratopetalum	×	*Fairrieanum*	85	Streathamense	0
20. Subg. Brachypetalum	×	*Godefroyae*	31	Don Carlos	0
21. Phacopetalum	×	Gowerianum (App. Chart II, #6)	19	Laure-Gower	0
22. Neuropetalum Subg. Brachypetalum	×	Graceae (App. Chart III, #5)	2	Grigna	0
23. Phacopetalum Neuropetalum	×	Harrisianum (App. to Chart III, #2)	72	gigas	8
24. Stictopetalum	×	*hirsutissimum*	33	Mulas	0
25. Phacopetalum	×	Holdenii (Chart I, #20)	6	Pauliae	0
26. Spathopetalum	×	*Hookerae*	26	Enfieldense	2
27. Neuropetalum	×	*insigne*	148	Umlauftianum	0
28. Phacopetalum	×	Io (App. to Chart III, #6)	15	Vanninii	0
29. Neuropetalum Phacopetalum	×	King Arthur (App. Chart III, #7)	9	Erl King	0
30. Cymatopetalum Neuropetalum	×	Lathamianum (App. Chart II, #9)	39	Pynaertii	0
31. Neuropetalum Cymatopetalum	×	Leeanum (App. Chart III, #3)	132	Magnei	0
32. Neuropetalum Cymatopetalum	×	Longwoodense (App. Chart III, #9)	18	Venizelos	0

*See footnotes Chart II for explanation.

Section of OTOPEDILUM (or other subgenera) used in cross		Species or hybrid used as parent		Resulting progeny	
33. PARDALOPETALUM	×	*Lowii*	20	MACFARLANIANUM (If Macfarlanei = 1)	0
34. ?	×	L'YSER	6	ALAIN GERBAULT	6
35. BLEPHAROPETALUM	×	*Mastersianum*	24	WILLIAM MATTHEWS	1
36. Subg. BRACHYPETALUM SPATHOPETALUM	×	MARSHALLIANUM (App. Chart III, #10)	1	HENRY GRAVES	0
37. PHACOPETALUM	×	MAUDIAE (Chart I, #2)	35	ALMA GAVAERT	11
38. SPATHOPETALUM NEUROPETALUM	×	MEASURESIANUM (App. Chart III, #11)	4	HEBE	0
39. Subg. ANATOPEDILUM Sect. CORYOPEDILUM PHACOPETALUM	×	MORGANIAE (App. Chart III, #12)	11	VENETIA	0
40. CERATOPETALUM CYMATOPETALUM	×	NIOBE (App. Chart III, #13)	28	WELLESLEYI	2
41. NEUROPETALUM	×	NITENS (Chart I, #3)	66	JOHNSONIANUM	0
42. Subg. BRACHYPETALUM	×	*niveum*	48	ANTIGONE	2
43. PHACOPETALUM Subg. ANATOPEDILUM Sect. CORYOPEDILUM	×	NUMA (App. Chart III, #14)	2	STANDENSE	0
44. PHACOPETALUM NEUROPETALUM	×	OENANTHUM (App. Chart III, #2)	28	BIJOU	0
45. MYSTROPEDILUM	×	*Parishii*	5	ELIZABETHAE	0
46. Subg. ANATOPEDILUM Sect. CORYOPEDILUM	×	*philippinense*	22	CHARLES STEINMETZ	0
47. PHACOPETALUM	×	PHLOGIODES (App. Chart III, #15)	1	NIGRUM	0
48. PHACOPETALUM SPATHOPETALUM NEUROPETALUM	×	POLLETTIANUM (App. Chart III, #16)	7	FABIA	0
49. Subg. BRACHYPETALUM	×	PSYCHE (App. Chart III, #17)	15	CONOPUS	0
50. Subg. ANATOPEDILUM Sect. GONATOPEDILUM	×	*Rothschildianum*	53	WIERTZIANUM	0
51. Subg. ANATOPEDILUM Sect. CORYOPEDILUM	×	*Sanderianum*	13	ULTOR	0
52. PHACOPETALUM Subg. ANATOPEDILUM Sect. CORYOPEDILUM	×	SELLIGERUM (App. Chart III, #18)	21	LADY LLANGATTOCK	0
53. BLEPHAROPETALUM PHACOPETALUM	×	SEMENTA (App. Chart II, #10)	8	CRASSIFOLIUM	0
54. CYMATOPETALUM	×	*Spicerianum*	62	RADIOSUM	2
55. Subg. ANATOPEDILUM Sect. CORYOPEDILUM	×	*Stonei*	27	NUMA	2
56. PHACOPETALUM	×	*superbiens*	39	EURYALE	5
57. PHACOPETALUM	×	SUPERCILIARE (App. Chart III, #15)	18	AUGUSTUM	2
58. PHACOPETALUM BLEPHAROPETALUM	×	SWANIANUM (App. Chart III, #19)	13	ROGERSII	0
59. BLEPHAROPETALUM	×	*tonsum*	33	MADAM BARBEY	0
60. SPATHOPETALUM	×	*venustum*	29	AUROREUM	2
61. PHACOPETALUM NEUROPETALUM	×	VERNIXIUM (App. Chart III, #20)	5	JULIEN COFFIGNIEZ	0
62. NEUROPETALUM	×	*villosum*	60	LURIDUM	0
					123

APPENDIX TO CHART III



Explanation of Plate

PLATE 31

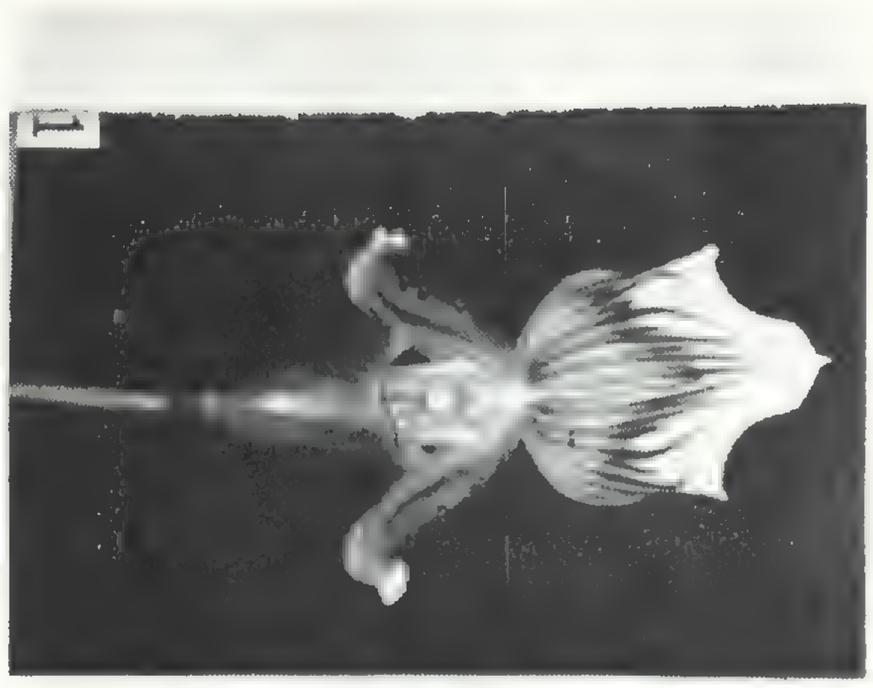
Flowers about ½; habits about ¼.

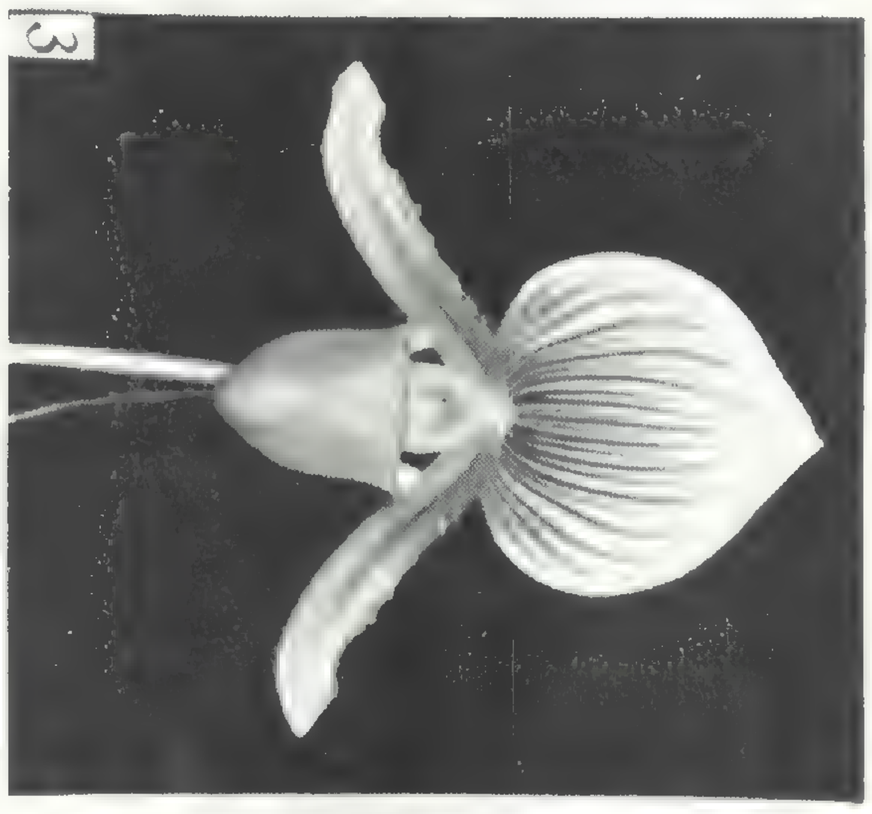
Figs. 1 and 2. *Paphiopedilum callosum.*

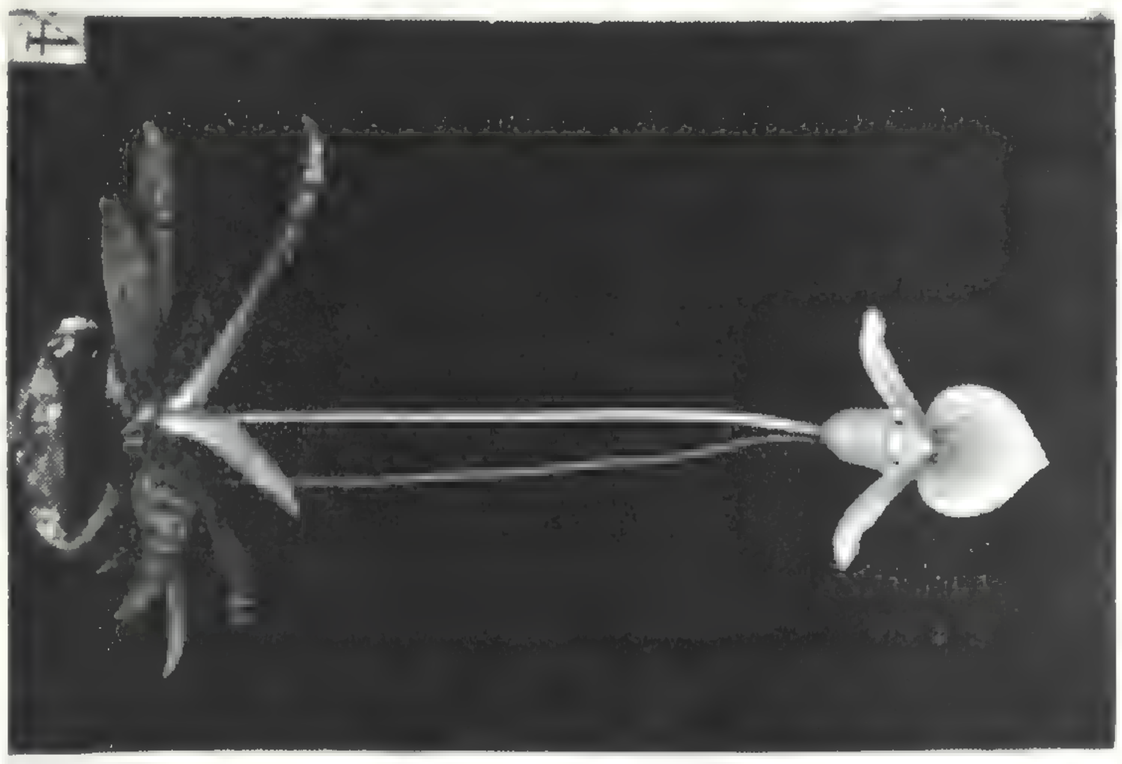
Figs. 3 and 4. *Paphiopedilum Maudiae* var. *magnificum.*

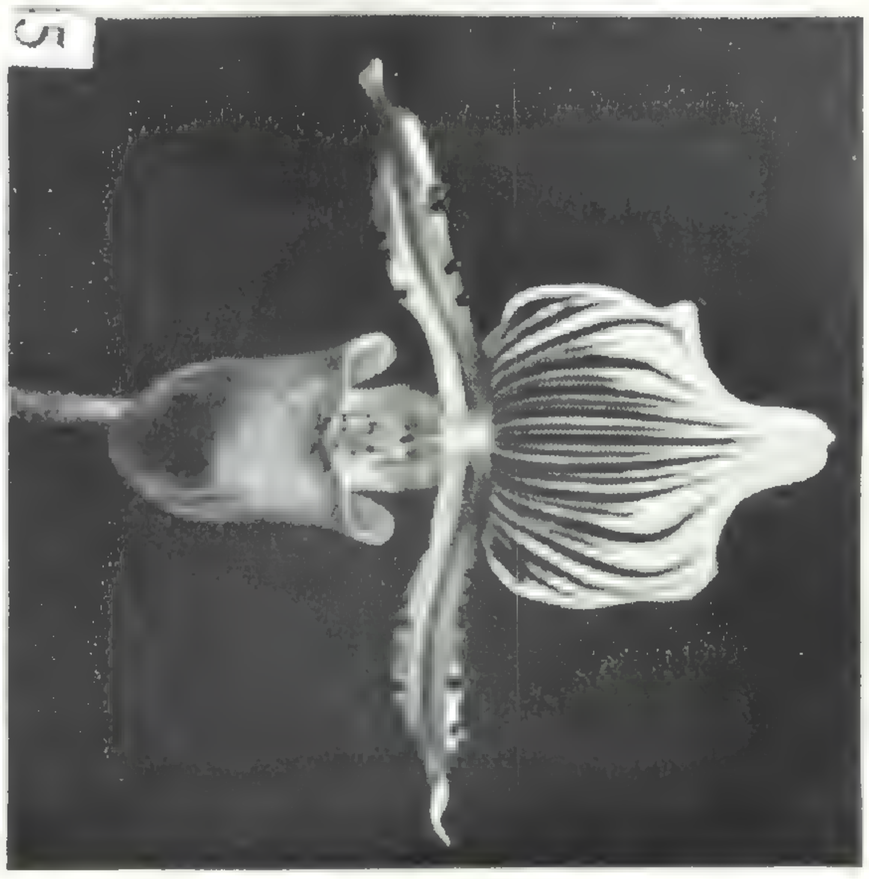
Figs. 5 and 6. *Paphiopedilum Lawrenceanum.*

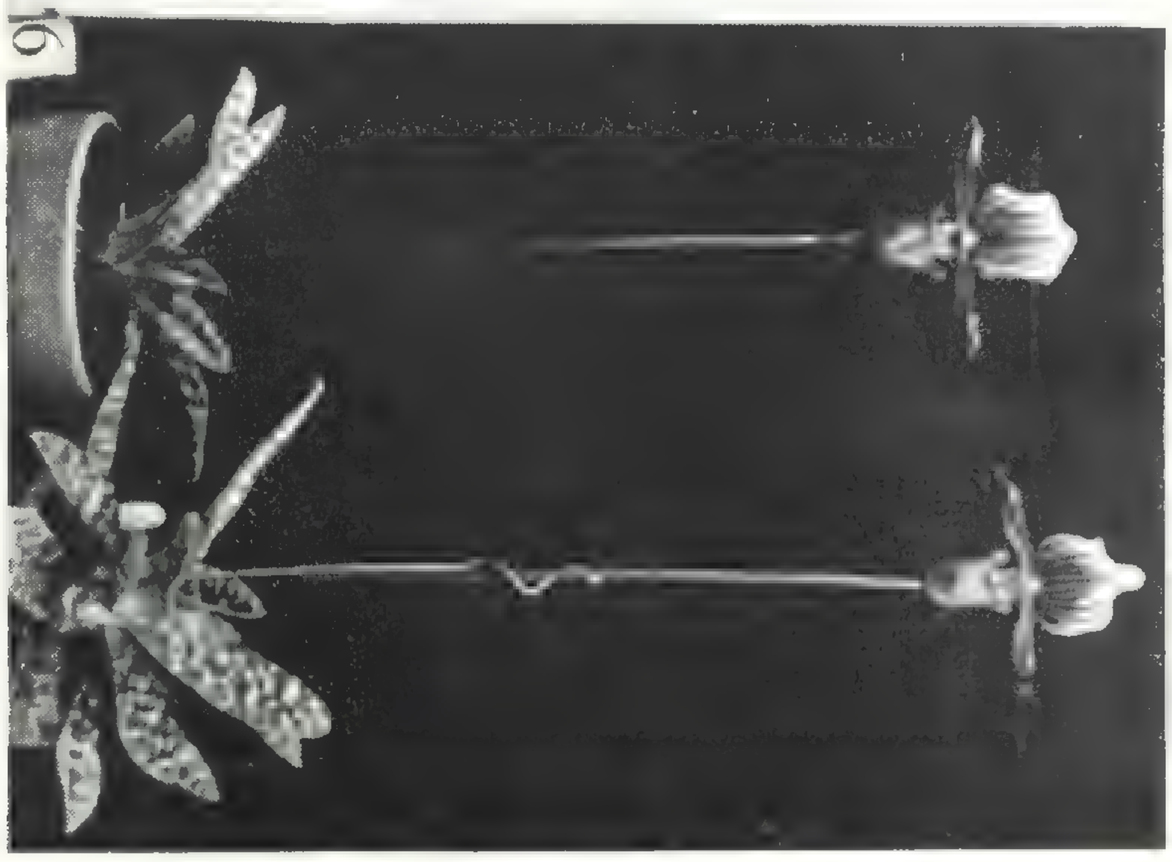
2


1


3


4


5


6

Explanation of Plate

PLATE 32

A. Anaphase in root-tip of *Paphiopedilum callosum*, × 1350. Aceto-lacmoid.

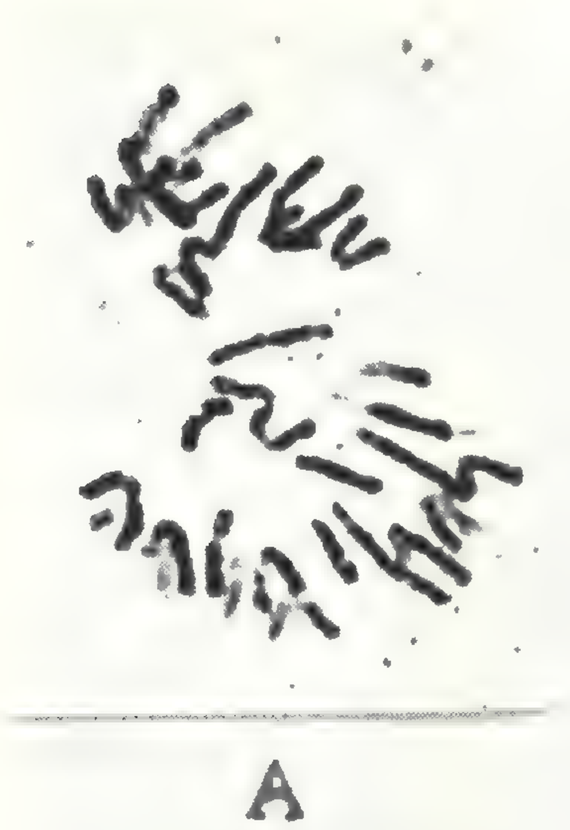
B. Anaphase in root-tip of *P. Laurenceanum*, × 1350. Feulgen.

C. Metaphase of root-tip of *P. Maudiae*, × 1350. Feulgen. The two homologues showing the inversion are marked.

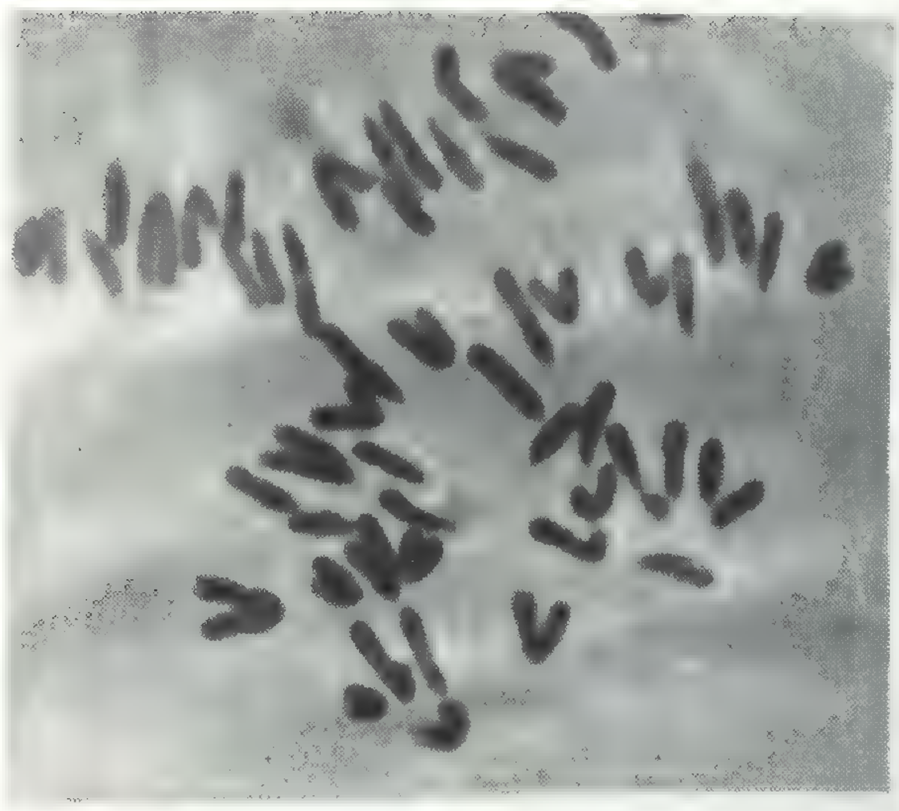
D. Camera-lucida drawing of the chromosome pair showing an apparently terminal inversion. These chromosomes are of intermediate length and have a prominent secondary constriction. The centromere is subterminal in one and median in the other (centromere marked with a line). Magnification × about 1800.

I. *P. callosum*. Metaphase I, 16 bivalents, × 1350. Crystal violet and safranin.

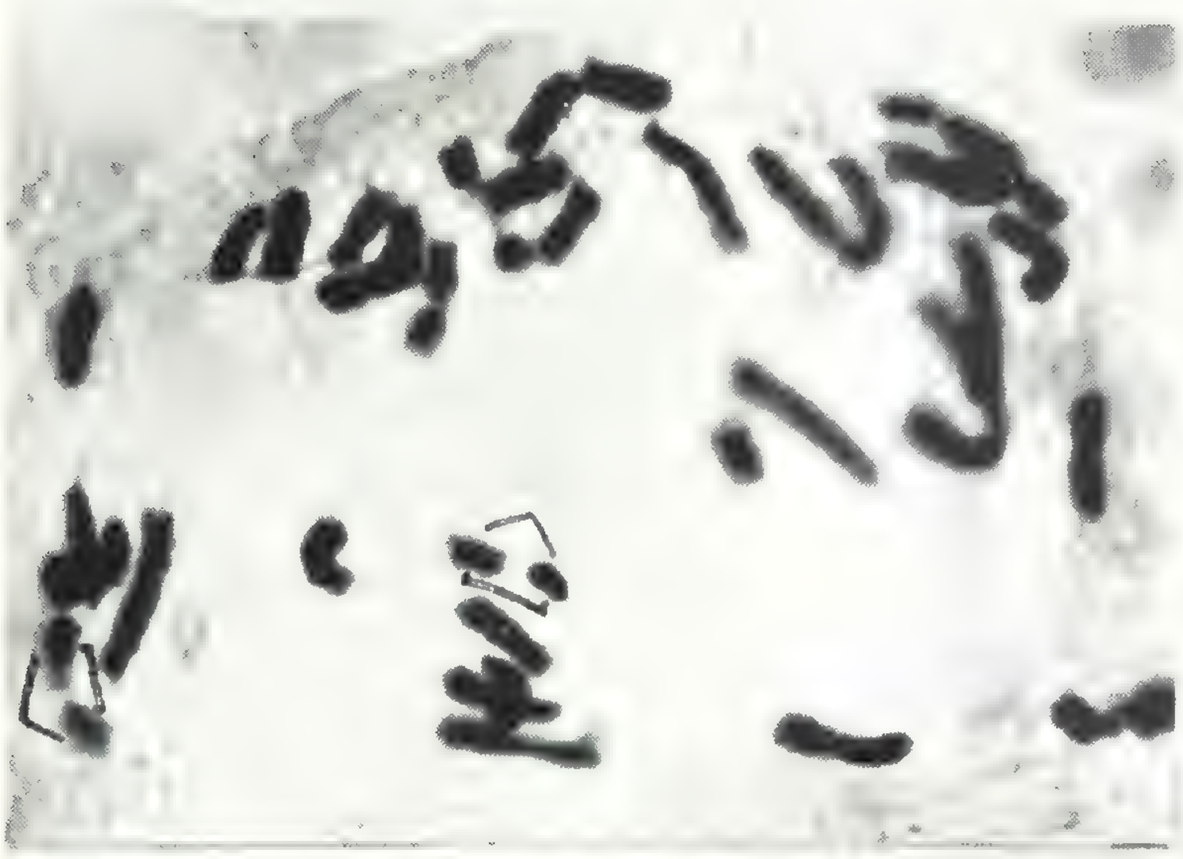
I. *P. Laurenceanum*. Metaphase II, 18 chromosomes, × 1350. Crystal violet and safranin.



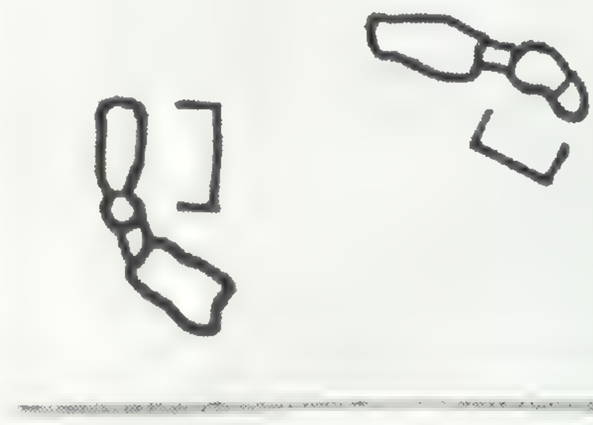
A



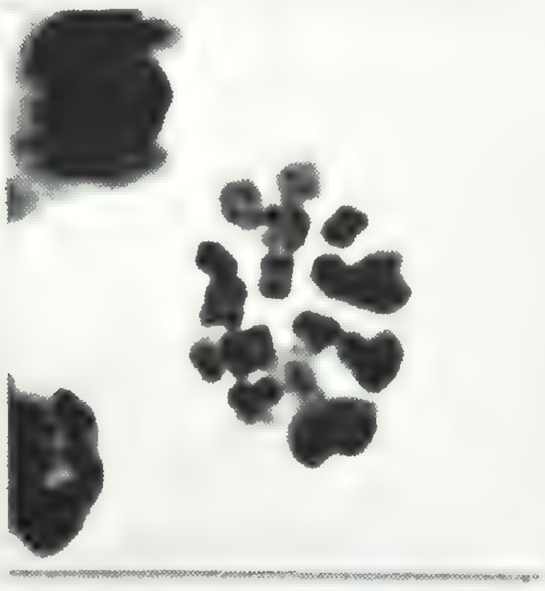
B



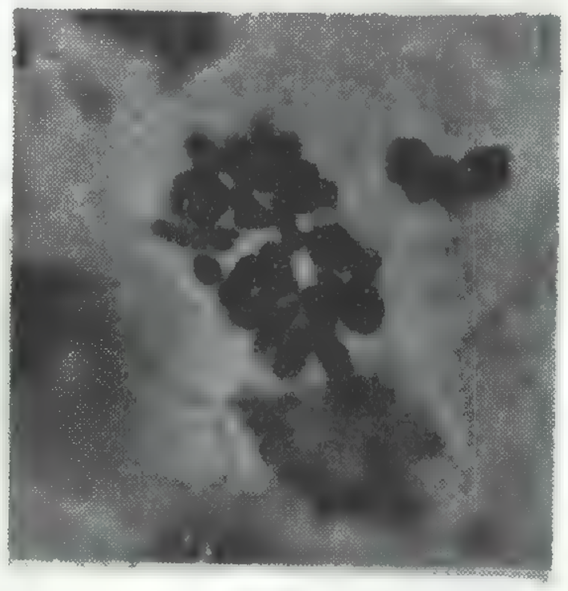
C



D



E



F

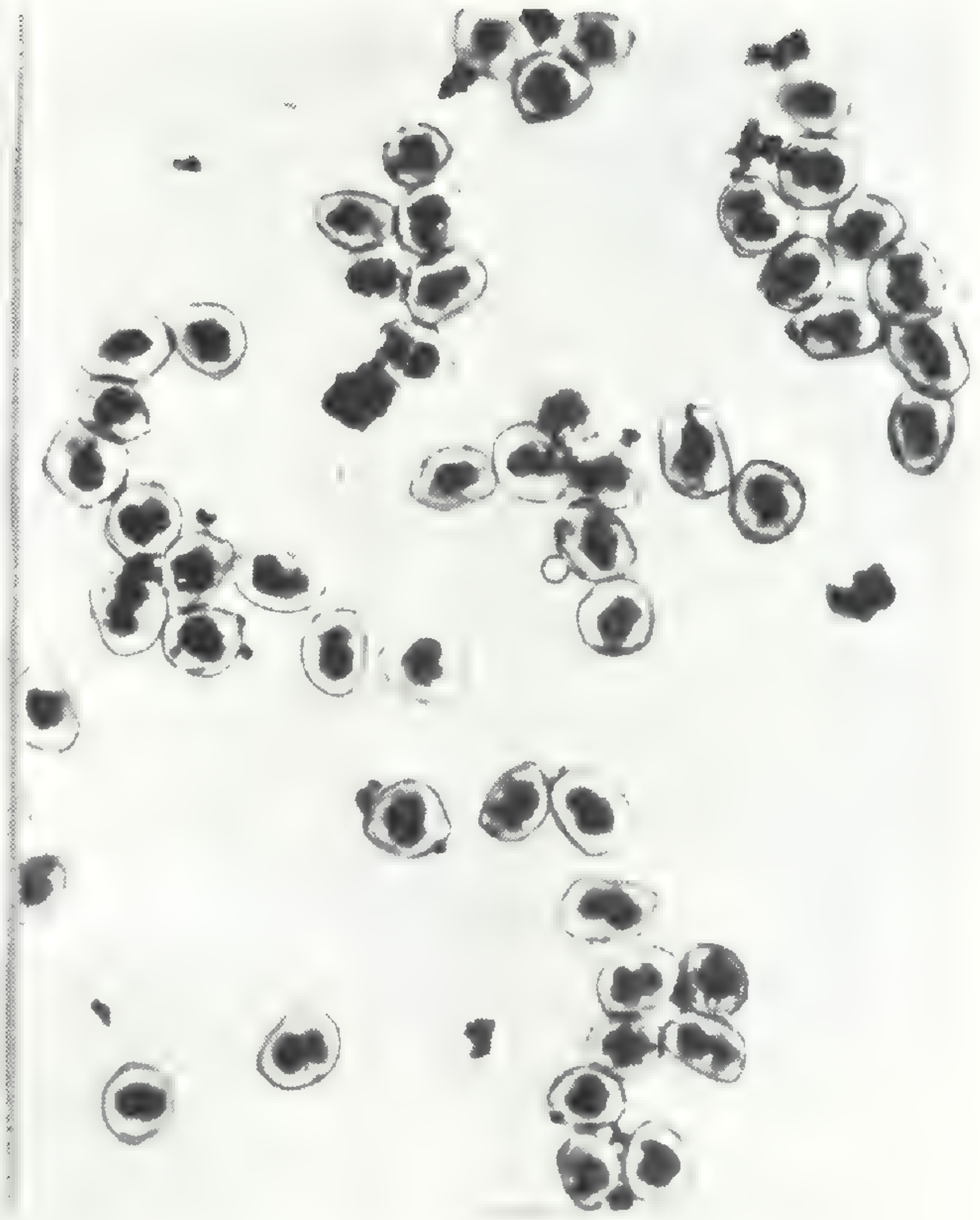
McQUADE—*PAPHIOPEDILUM MAUDIAE* HORT.

Explanation of Plati

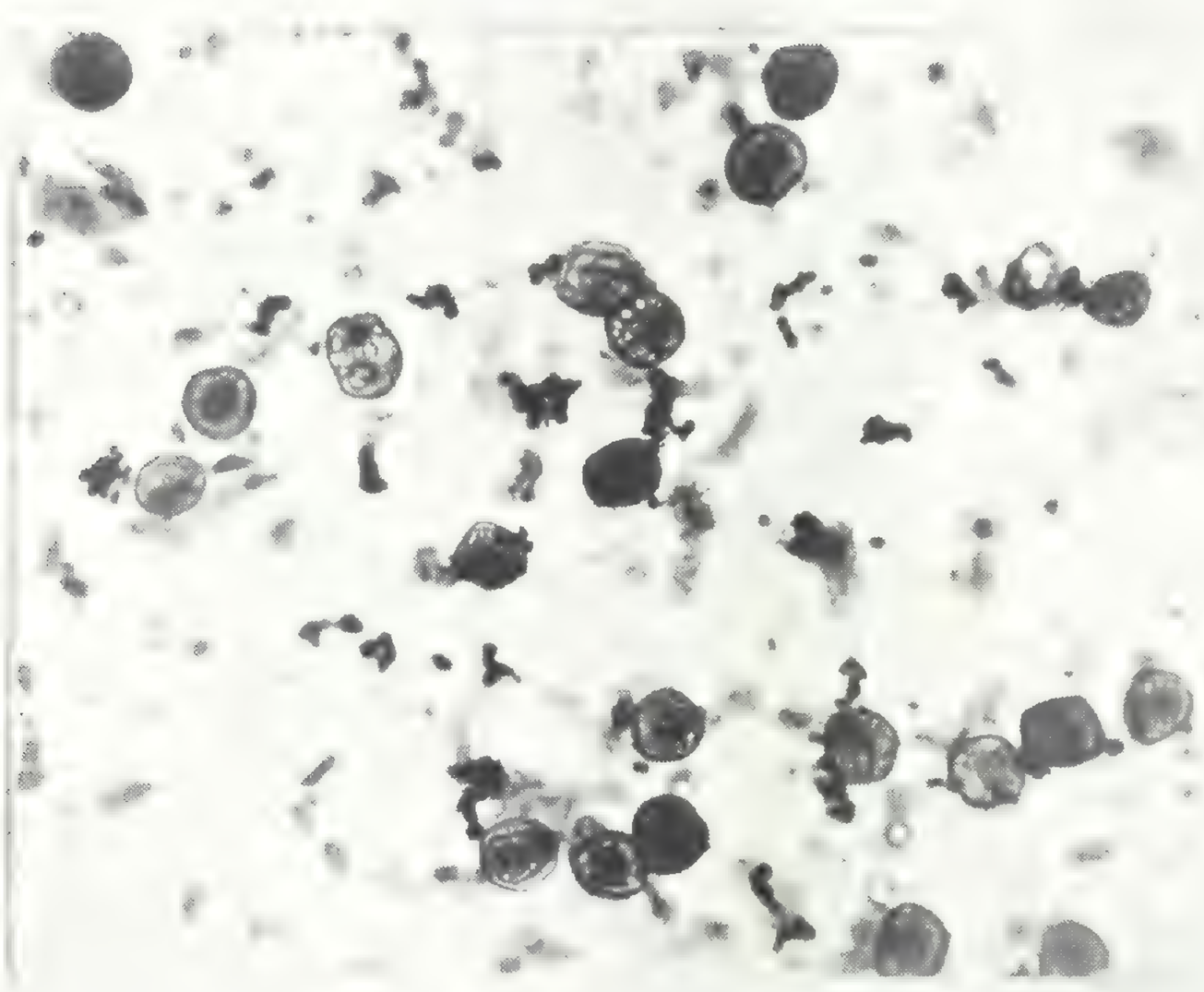
PLATE 33

Pollen of *Paphiopedilum callosum*, of *P. Lawrenceanum*, and of *P. Maudiae*, about 250.

P. callosum



P. Lawrenceanum



P. Maudiae

Explanation of Plate

PLATE 34

Paphiopedilum Maudiae Hort.

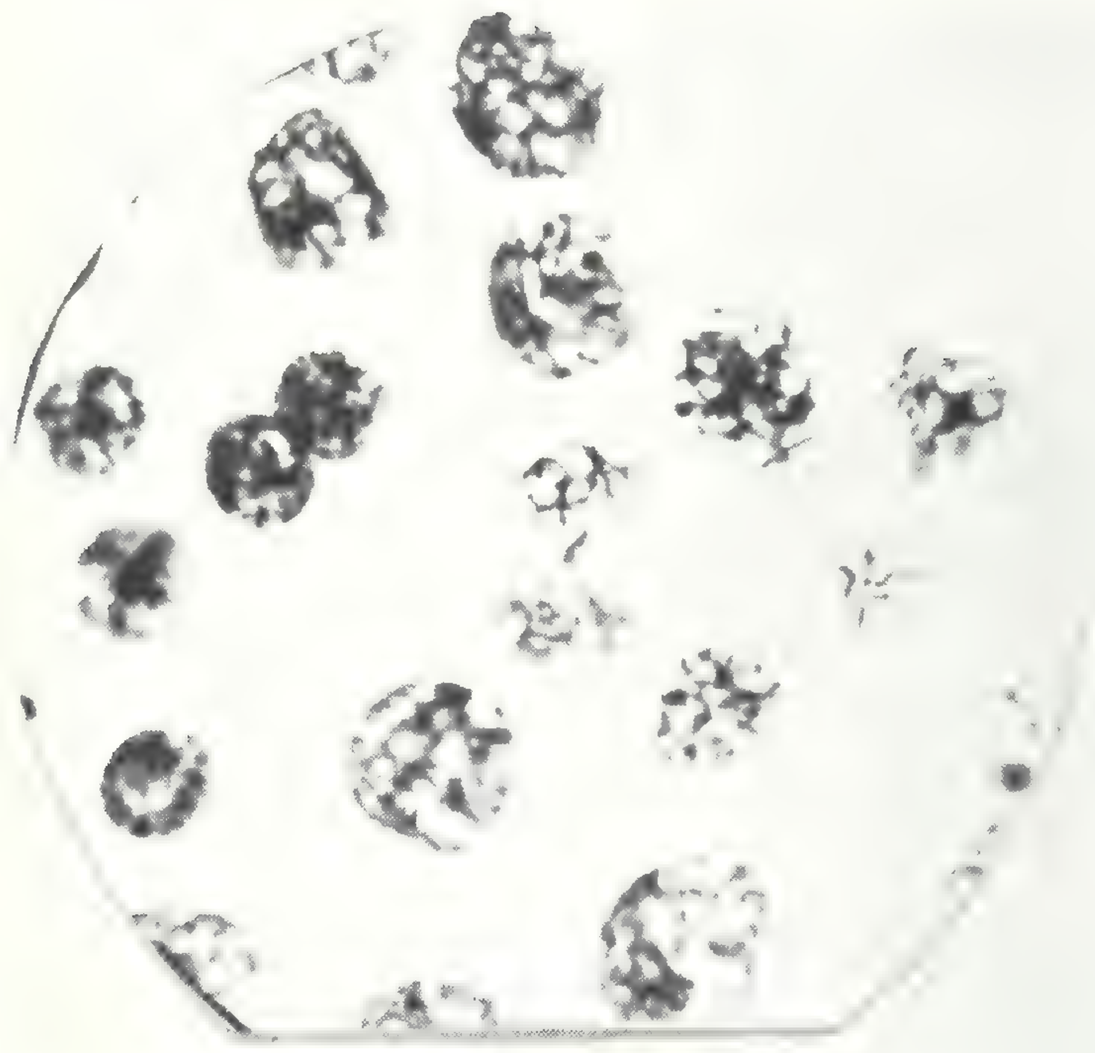
A. Pachytene-early diplotene, × about 1350.

B. Metaphase I, 17 bivalents, × about 650.

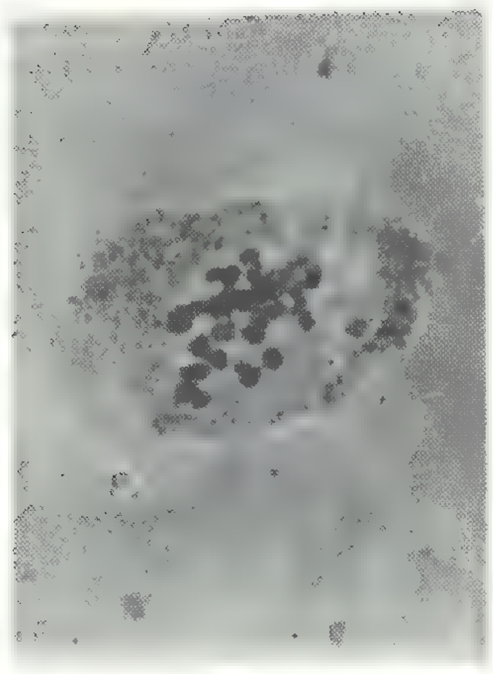
C. Anaphase I, bridge and fragment, × about 650.

D. Metaphase II, × about 750.

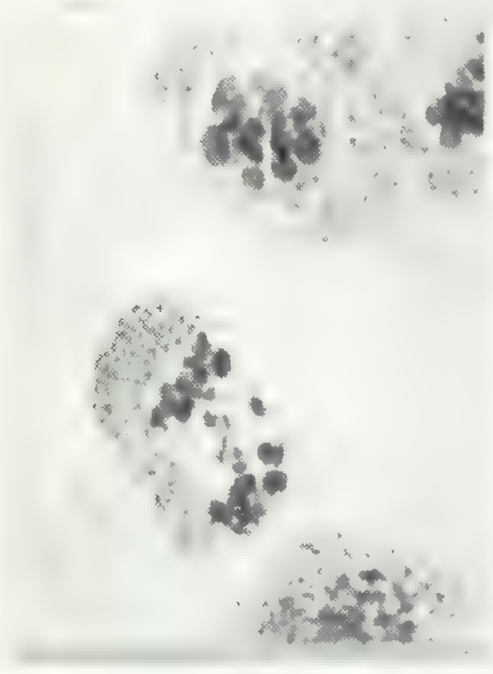
E. Tetrads (note micro-grain), × about 700.



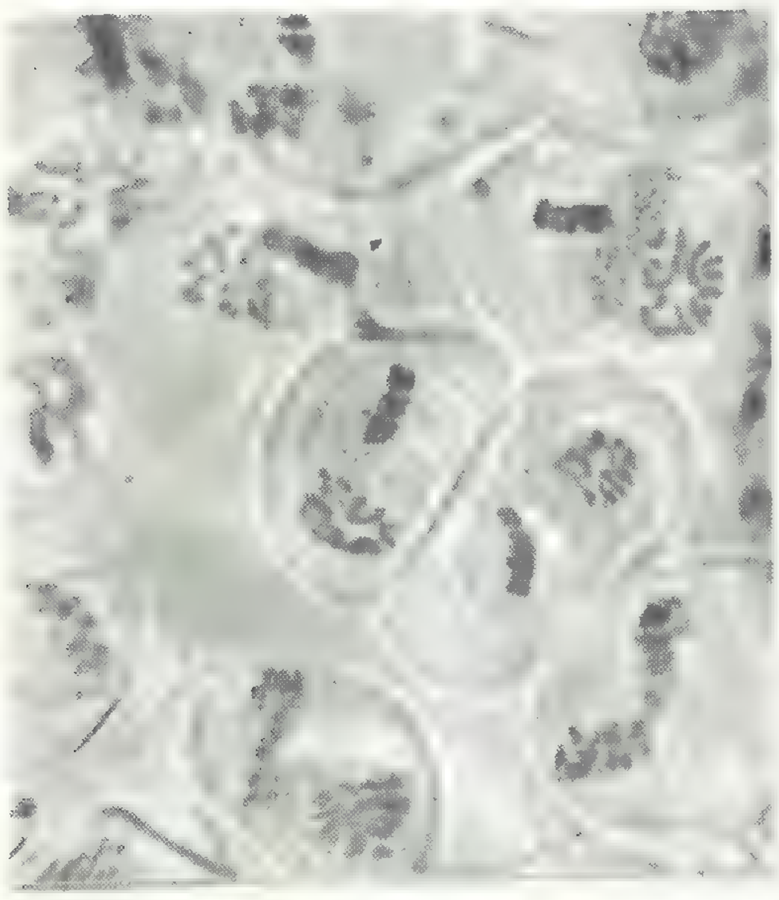
A



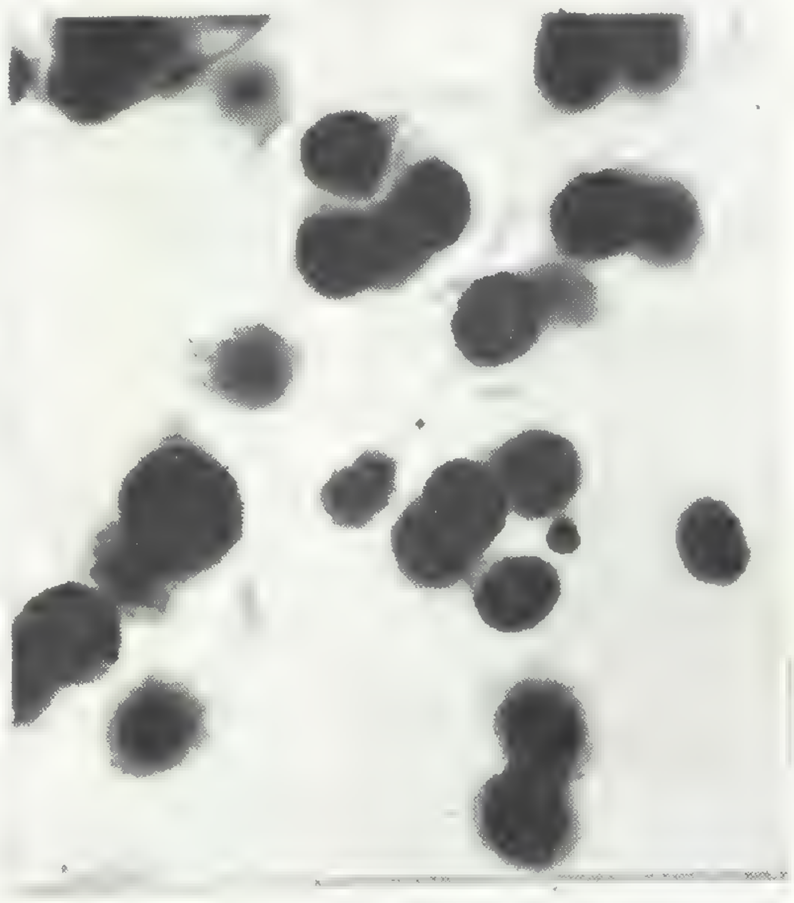
B



C



D



E

McQUADE—*PAPHIOPEDILUM MAUDIAE* HORT.

STEGNOSPERMA: A NEW SPECIES AND A GENERIC COMMENTARY

DAVID J. ROGERS

The genus *Stegnosperma* (Phytolaccaceae) has been considered monotypic since Walter's treatment for Engler's 'Pflanzenreich'[1]. However, an examination of specimens in the major North American herbaria shows the inclusive species S. *halimifolium* Benth. of Walter to be rather heterogeneous. Actually, three species exist, two of which have been described and published, the third noted by S. Watson on an herbarium label but never published. A description of the third species is provided here and is named for Dr. Watson.

STEGNOSPERMA **Watsonii** D. J. Rogers, n. sp. Frutices aut scandentes aut crassi patulique 1–5 m. alti, 1–5 m. diam., cortice griseo vel rufo-brunneo. Folia anguste spathulata vel elliptica emarginata vel rotunda vel acuta 1.0–3.5 cm. longa 0.5–2.5 cm. lata, petiolo 0.1–0.3 cm. longo. Inflorescentia cymulis axillaribus aut terminalibus 1–8-floris; calycis lobis ellipticis vel ovatis 0.3–0.7 cm. longis 0.2–0.4 cm. latis; petalis ovatis rotundatis basi abrupte constrictis; fructu capsula 5-loculata plerumque in 5 valvis dehiscente; seminibus plerumque 5 aliquando 4 ovoideis vel ellipsoideis circa 0.3 cm. longis 0.2–0.3 cm. latis, cicatrice funiculari laterali, raphe in jugum dorsalem, testa levi fulgenti rufo-brunneo.

Sprawling vine or coarse spreading shrub, 1–5 m. tall, 1–5 m. diameter spread; bark gray to reddish brown. Leaves narrowly spathulate to elliptic, emarginate to rounded to acute, 1.0–3.5 cm. long, 0.5–2.5 cm. wide, petiole 0.1–0.3 cm. long. Inflorescence of axillary or terminal 1- to 8-flowered cymules; calyx lobes elliptic to ovate, 0.3–0.7 cm. long, 0.2–0.4 cm. wide; petals ovate, rounded, abruptly constricted at base; fruit a 5-celled capsule, usually dehiscing by 5 valves; seeds usually 5, occasionally 4, ovoid to ellipsoid, about 0.3 cm. long, 0.2–0.3 cm. wide, funicular scar lateral, raphe on a dorsal ridge, testa smooth, shiny, reddish brown.

MEXICO: BAJA CALIFORNIA: *Wiggins 7681.* SINALOA: *Jones s. n.* SONORA: *Abrams 13343; Coville 1646; Dawson 1058; Drouet, Richards & Alvarado 3443; Ferris 8741; Gentry 2195, 2975; Goldman 399; Keck 4067; LeRoy s. n.; Lumholtz 9; McGee s. n.; William Palmer 1226* (HOLOTYPE in Herb. Missouri Botanical Garden, isotypes in Herb. N. Y. Bot. Gard. and U. S. Nat. Herb.); *Pringle s. n.; Rose 1211, 1211a; Rose, Standley & Russell 12390, 12566, 13138, 13231, 15047; Shreve 5992; Wiggins 6247.*

This species seems to be most closely related to S. *halimifolium* Benth., from which it may be distinguished by its scattered, few-flowered cymules, its ovate, abruptly constricted petals, and by its lateral funicular scar.

Stegnosperma Watsonii grows on hillsides along rivers, thickets in palm groves, thorny foothills, from sea level to 300 meters. It flowers from about the first of February through March, and fruits from the last of February through April.

That there are actually three species of *Stegnosperma* is most easily demonstrated by the following key:

---

[1] Walter in Engl. Pflanzenr. IV, 83:124. 1909.

Issued November 30, 1949.

A. Inflorescence a terminal, many-flowered racemiform thyrse; petals rather gradually narrowed to the base.
  B. Sepals linear to elliptic; petals linear to spathulate; capsule dehiscing by 3 to 4 or rarely 5 valves, usually with 1 to 3 seeds; seeds with a lateral to sub-basal funicular scar, the raphe on a flattened dorsal surface.....*S. cubense*
  BB. Sepals ovate; petals ovate to elliptic; capsule dehiscing by 5 valves, usually with 5 seeds; seeds with a basal funicular scar, the raphe on a dorsal ridge.....*S. halimifolium*
AA. Inflorescence an axillary, 1- to 8-flowered cymule; petals abruptly constricted at the base .....*S. Watsonii*

STEGNOSPERMA CUBENSE A. Rich. in Sagra, Hist. Nat. Cuba 10:309; 12:*tab.* *44*[3]. 1845.

[*Trichilia*] *scandens, foliis simplicibus, ovatis alternis, etc.* A. Robinson ex Lunan, Fl. Jam. 2:319. 1814.

Trichilia scandens Lunan ex B. D. Jackson, in Index Kewensis 2:1105. 1895. Based on the preceding.

Stegnosperma scandens (Lunan ex B. D. Jackson) Standley, in Field Mus. Publ. Bot. 23:6. 1943.

Stegnosperma halimifolium of authors, not Benth.

MEXICO: TRES MARIAS ISLANDS: *Fisher s. n.; Howell 10409; Maltby 45; Mason 1702; Nelson 4185; Solis 4, 22, 45.* REVILLA GIGEDOS ISLANDS: *Mason 1846.* SINALOA: *T. S. Brandegee s. n.; Eyerdam & Beetle 8652; Lamb 465; Mexia 45, 152, 1095; Ortega 4480, 5150, 5649, 6453, 7232, 7488; E. Palmer 1503; Rose s. n., 1535; Rose, Standley & Russell 13721.* NAYARIT: *Ferris 5300; Nelson 4340.* COLIMA: *Goldsmith 99; Jones 13; E. Palmer 1280.* MICHOACAN: *Hinton 12627; Leavenworth & Hoogstraal 1394.* MEXICO: *Hinton 3764.* GUERRERO: *Hinton 5431, 5719, 5962.* OAXACA: *Matuda 0664; Nelson 2597; Orcutt 3307.* CHIAPAS: *Matuda 2808; Morley 710.* VERA CRUZ: *Purpus 8059, 10080, 13066.*

GUATEMALA: ESCUINTLA: *Salas 378.* SAN JOSE: *Worth, Morrison & Horton 8632.* RETALHULEU: *Standley 87707.* SAN MARCOS: *Steyermark 37762, 37773, 37881.* SUCHITEPEQUEZ: *Steyermark 47825.* ZACAPA: *Standley 74066; Steyermark 42084.*

EL SALVADOR: LA LIBERTAD: *Standley 23219.*

NICARAGUA: CHINANDEGA: *Baker 2065.* MANAGUA: *Chaves 262; Garnier 1071; Maxon, Harvey & Valentine 7215.*

CUBA: HABANA: *Ekman 13493.* PINAR DEL RIO: *Baker & Van Hermann 4247; Ekman 13039, 16733; Leon & Roca 7132, 8810; Shafer 11140, 11148; Wilson 11400, 11404.* WITHOUT LOCALITY: *Wright 2027.*

JAMAICA: vicinity of Spanish Town, *Britton 3062.* Healthshire Hills, *Harris & Britton 10522.*

DOMINICAN REPUBLIC: Beata Island. *Fairchild 2605, 2606, s. n.; Ostenfeld 319.* Massif des Cahos, *Ekman H9095.* BARAHONA: *Ekman H6961.* SIERRA DE OCOA: *Ekman H13360.* WITHOUT LOCALITY: *Bertero s. n.*

PUERTO RICO: Asomante, *Horne & Britton 9628.*

This species, although placed in synonymy under S. *halimifolium* by Walter[2], is sufficiently distinct to be maintained. The description and plate provided by Richard demonstrate its characters accurately. Further characters which support my interpretation are found in the seed. These characters are used in the key.

An interesting nomenclatorial problem concerning this species arose when Standley[3] made an apparently valid transfer of a "species" of *Trichilia* ascribed to Lunan by B. D. Jackson in 'Index Kewensis'[4]. Lunan's "publication" of A. Robin-

[2] Walter, loc. cit.
[3] Standley, in Field Mus. Publ. Bot. 23:6. 1943.
[4] B. D. Jackson in Index Kewensis 2:1105. 1895.

son's manuscript description of a new species of *Trichilia* was as a polynomial. Jackson's interpretation of the name as a binomial possibly could be explained by a method used in early printing in which the first word of a page was placed at the bottom of the preceding page on a line by itself. In this case, the first word to appear in the first sentence at the top of page 320, Lunan's Fl. Jam. Vol. 2, and accordingly at the bottom of the preceding page was "*scandens.*" I do not think that Lunan intended a binomial since he did not mention "*scandens*" as a species in his Classical Index of this work although other properly published binomials are listed, nor did he use the same form in his discussion of the plant in question as he consistently used throughout the text for species designation.

STEGNOSPERMA HALIMIFOLIUM Benth. Bot. Voy. Sulph. 17:*pl. 12.* 1844 (as *halimifolia*).

MEXICO: BAJA CALIFORNIA: *T. S. Brandegee s. n.; Carter 2725; Carter, Alexander & Kellogg 1980, 2115, 2497; Collins, Kearney & Kempton 186; Epling & Robison s. n.; Ferris 8617; Gentry 4032, 7603, 7864; Hammerly 102; Harvey 609; Johnston 3166, 3354, 3488, 3512, 3593, 3825; Jones 24481, 27465; Nelson & Goldman 7147, 7249, 7323, 7395, 7502; E. Palmer 31, 258, 400, 870; Purpus s. n., 5; Rose 16289, 16415, 16616, 16690; 16924; 16947; Shreve 6973; Wiggins 5415, 5651, 6070, 7793; Xantus 9b.* SONORA: *MacDougal & Shreve 40, 47; Pringle s. n.*

The generic ending of Bentham's specific epithet has been altered to comply with the International Rules of Botanical Nomenclature, Section 14, Art. 72 (2).

As I have interpreted this species, it occupies a rather narrow range in Baja California and occasionally in the adjoining state of Sonora, Mexico.

I have been able to examine specimens from several of the major herbaria of the United States, but have not seen the type specimens nor any other material from Europe.

The herbaria where specimens have been obtained for study are as follows: Gray Herbarium of Harvard University, Chicago Natural History Museum, Missouri Botanical Garden, New York Botanical Garden, University of California at Berkeley, and the United States National Herbarium.

I wish to acknowledge my indebtedness to the curators of these institutions.

NUCELLANGIUM, A NEW GENUS OF FOSSIL SEEDS PREVIOUSLY ASSIGNED TO LEPIDOCARPON

HENRY N. ANDREWS, JR.

Among the more abundant fossils found in the Iowa coal balls are the highly unique "seeds" which have been named *Lepidocarpon glabrum*. These were described by W. C. Darrah in 1941, and in a more recent publication (1949) the same author has continued the discussion with descriptions of included structures which are claimed to be gametophytes and embryos. It is the purpose of this paper to add somewhat to the information given in the published accounts, to point out what appear to the present writer as erroneous statements of fact, and to correct the corresponding conclusions. The fossil is not referable to any known genus, and a new generic name, *Nucellangium*, is proposed herewith for its reception.

Origin of the specimens.—

The specimens on which the present descriptions are based were collected by Mr. Frederick O. Thompson from the Urbandale coal mine located on the western outskirts of Des Moines, Iowa, the exact location having been given in the results of a previous study from this laboratory (Andrews and Kernen, 1946). It should be noted that these specimens and the ones described by Darrah come from the same locality, and through the cooperation of Dr. Elso Barghoorn I have also been able to study a series of similar preparations from the Botanical Museum of Harvard University. There is, therefore, no possibility of confusion in the identity of Darrah's specimens and the ones on which this account is based.

The material is from beds of Middle Pennsylvanian (Des Moines) age; unfortunately the precise stratigraphical equivalence of the Urbandale coal is not known but presumably the material is a little younger than floras known from Illinois No. 6 coal or from above the upper Freeport coal of Pennsylvania.

General introduction to the nature of the fossils.—

We are involved in this discussion with two sets of fossil plants, the first being ovoid bodies presenting certain anatomical characters which lend some justification to their being considered as seeds, and the second less regularly shaped bodies with highly distinctive convolutions extending into their interior which are alleged to represent gametophyte and sporeling.

Certain competent botanists who have examined the fossils in my collection have expressed doubt that the two phases or forms belong to the same species. Mr. Darrah has based his case on the supposition that they represent different growth stages of the same organ. I agree with him to that extent yet it must be remembered that it is not beyond the realm of possibility that we are wrong in this belief.

It seems most convenient to refer to these two forms as *proliferated* and *normal* depending on whether they do or do not contain the supposed sporelings. In view

Issued November 30, 1949.

of the incomplete nature of the previously published accounts it will be necessary to present rather detailed descriptions of the two phases.

I have little doubt that many morphologists will take issue with the usage of terms as they are applied to these fossils. It is becoming clear, however, in groups such as the psilophytes and early coenopterid ferns, that the fossils are not going to make a special effort to comply with our preconceived terminology. It is hoped that the following pages contain descriptions that may be readily comprehended, but I believe that these fossils present structures which do not correspond precisely with known morphological entities.

Insofar as the evidence allows it seems clear that the fossils are sporangia that may or may not have been integumented. It is not known how they were borne on the parent plant and Darrah's restoration of the "strobilus" (1949, fig. 39) is based, so far as I am able to judge, on the supposed general lycopod affinities of the fossil rather than on conclusive evidence. There is a trace of conservatism in the caption to that figure which reads, "Sporophylls not sufficiently known to warrant reconstruction." The fact is that nothing whatsoever is known of the supposed sporophylls.

The general organization of the fossil, with its vascularization and complicated wall structure, seems to allow a closer comparison with a cordaite seed than with a lycopod sporangium. We shall return to such speculations on a later page.

The fossil will be referred to in the following pages as a *sporangium*, as a *nucellus*, or as an (unintegumented) *seed*. The last term is used advisedly and as a matter of convenience, although it seems probable that at least the specimens containing a "seed megaspore" did function as such. It seems most expedient to present first a detailed description of the "normal" fossils and then consider the morphology of the principal structures involved.

The "normal" seeds.—

These are very abundant in the Urbandale coal balls as well as in those from other localities which probably represent the same or a close horizon. In many of the coal-ball specimens examined a half dozen or more are exposed in a single saw cut and, due to the distinctive structure and preservation of the epidermal layer, they are often partially exposed on the broken surfaces of the petrifactions. It is occasionally possible to isolate the seeds intact from the surrounding matrix. While the following description is supplemented by observations on dozens of specimens it is based primarily on a series of transverse sections prepared through a single specimen.

Although there is some variation in the size of the specimens it is not great. They are broadly ovate (figs. 1, 2), averaging 12 mm. long, and in the median region the large and small diameters are 9.5 by 6 mm. Many specimens, particularly the more poorly preserved ones, are crushed and distorted, yet there can be no doubt that the shape and dimensions as given here represent the life form of the seeds.

At one end of these slightly elongated structures, which we will refer to as the proximal end, there is a tiny circular "hilum" scar (fig. 5) representing the point of attachment. At the other end, which will be referred to as the distal end, the seed tapers to a blunt point. Fairly conspicuous ridges lead to this point from the median region of the seed, following the narrow lateral faces. The specimens shown in figs. 1 and 2 present the broad side of the seed and the ridges here form the outline of the photo of the upper half of the seed. The hilum scar may be seen at the proximal end in fig. 1 and the blunt point at the opposite extremity.

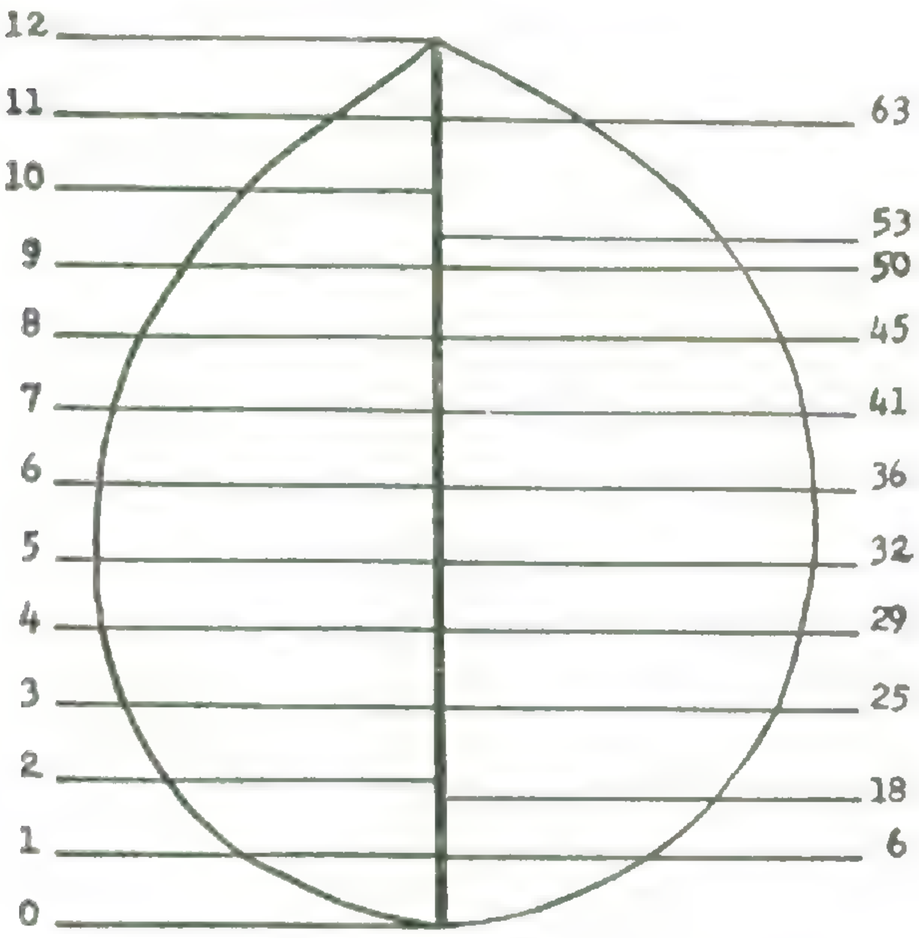
A series of peel preparations has been made by first carefully smoothing a flat surface at the hilum end. Seventy successive peels were then made to within less than a half mm. of the distal end. Particular care was taken to obtain a nearly perfect serial series at the hilum end in order to trace accurately whatever vascular system might be present. When it became evident after working through about one quarter of the length of the specimen that sudden changes in anatomy were no longer taking place the sections were taken further apart in the median region.

It is perhaps apparent that this is a case in which the peel technique is quite indispensable, for it would be only through the greatest good fortune and the use of numerous well-preserved specimens that somewhat comparable results could be obtained by reliance only on ground sections. It is probable that if the specimen had been properly imbedded even better preparations could have been made. However, they were generally removed with little difficulty by using a sharp razor under the low power of a dissecting microscope. Occasionally the epidermis was partially destroyed but since this remains constant in structure from one end to the other there was no loss. Text-fig. 1 indicates the approximate position from which the respective peels were taken.

To present an effective description of *Nucellangium* this series of preparations will be followed from proximal to distal end. It may be an aid in following the discussion to note at the outset that three characters set this fossil apart from previously described species of *Lepidocarpon*. These are: a well-developed vascular system with two strands running nearly the entire length of the seed; a thick complex wall including an inner sclerotic layer; and a mode of attachment unlike that of the radially elongated sporangia of other species of *Lepidocarpon*. This combination of characters, and particularly the vascular system, clearly prevents the inclusion of the fossil in that genus.

In the first peel prepared, which does not quite reach the inner limit of the epidermis, the central vascular strand may be distinguished. It is circular in transverse section and is composed of a considerable number of conducting elements (fig. 8). It is apparently purely tracheidal, no parenchyma cells having been observed. The conducting elements of this basal strand, as well as those of the lateral traces, are distinctive in that they are thin-walled, follow a slightly sinuous course, and the bands composing the secondary thickenings are fine and delicate, a condition, judging from the generally good preservation through the specimen, that is natural and not the result of decay. It is not possible to determine

whether the secondary thickenings were of a typical annular or scalariform nature; if the latter, it seems evident that the border of the thickenings was not strongly developed.



Text-fig. 1. Diagrammatic longitudinal view presented as an aid in following the description of the series of transverse peels described on the accompanying pages. Figures at left are millimeters; figures at right represent peel numbers.

Text-fig. 2. Diagrammatic median longitudinal section through the major axis of the seed showing the entrance of the vascular strand at the base and the course of the two branch traces through the length of the wall.

At peel No. 4 a disturbance of the thin-walled parenchyma surrounding the strand suggests a departing trace and when peel No. 6 is reached the tracheids of a branch trace may be observed, not actually leaving the strand but more than half way to the periphery of the seed. At first it was thought that the point of departure had been missed but in the next peel the trace was noted both departing (fig. 6) and in the outer region, as noted above. It is evident, as shown in fig. 10, as well as in text-fig. 2, that the trace dips down slightly after leaving the central strand to follow its course up through the seed. In peel No. 7 the departure of a second trace appears on the opposite side of the central strand.

No other branch traces were observed although a careful search was made, since in his original description Darrah (1941) notes, with reference to the vascular system: "At the proximal end of this seed-like sporangium there is a vascular trace which forks twice, but the four branches quickly exhaust themselves. The bifurcations are at right angles to each other, and by serial sections it has been observed that the two forkings take place one above the other." (p. 97).

The presence of these vascular strands, as I have described them, is of the greatest importance since they are typically absent from lycopod sporangia. It is understandable that they might be readily overlooked in longitudinal sections but

I cannot feel that there is adequate excuse for failing to observe them in the serial sections Darrah indicates were prepared (1941, p. 85).

The pair of traces continues to within less than one half mm. of the distal end of the seed and may be clearly observed in most of the peels throughout the length of the seed; and in the specimen described here there is no suggestion of a second pair of traces. A possible explanation of the *apparent* departure of such will be offered below.

It is clear from all of these transverse peels, with the exception of the basal two or three, that the seeds are bilaterally symmetrical in their anatomy as well as in their gross external form. Taking as an example a nearly median section (fig. 16) the ovate form of the fossil is evident and the two traces may be seen at either end of the great diameter, the traces in this peripheral region occupying a position in extensions of the inner sclerotic layer. Figure 7 shows the trace rather well at a point where it and the surrounding tissues are quite well preserved.

For the purpose of considering the extra-vascular structure of the seed a nearly median point will be taken where a typical sequence of the tissues is displayed. Selecting peel No. 34 (figs. 12, 16) the following may be clearly defined:

The thick-walled, palisade-like epidermis (fig. 9) forms the outer cell layer of the seed over its entire surface with the exception of the hilum scar at the base. These cells are arranged with their long axis approximately parallel to a radius of the seed. They are uniform in size and shape, being about 125 μ long and, when observed in surface view, about 25 μ in diameter. These cells also present an interesting preservation problem. They seem immune to the action of hydrochloric acid, unsuccessful attempts having been made to etch the outer face in order to obtain surface peels. Apparently they are little, if at all, mineralized. It is not surprising that with such an external tissue, so seemingly resistant to an infiltrating mineral solution, the more delicate internal tissues are poorly preserved in most specimens.

Within this epidermal layer is a broad zone of nearly isodiametric, rather thin-walled cells (the outer parenchyma, o. p. of figs. 12, 16). As may be noted in the photos this tissue comprises a major portion of the sporangium wall as a whole. There is a tendency for approximately the outer third of this tissue to have somewhat thicker cell walls than the inner region although there is no sharp distinction into two zones. It is highly significant to the discussion of the morphology of the seed to note that this is clearly *in continuous tissue connection with the conspicuous columnar epidermis.*

Forming a third layer is a very prominent, dark and semi-sclerotic tissue (inner sclerotic layer, i. s. of figs. 12, 16). The term "sclerotic" is perhaps misleading although the cells are somewhat thicker walled than those of the outer parenchyma.

It will be noted (fig. 12) that the cells of this tissue increase appreciably in diameter towards the inner periphery, and they are longitudinally elon-

gated, being at least twenty times as long as they are broad. Where the preservation is good, and nearly perfect longitudinal sections are obtained, the cell walls appear to be strongly pitted. The end walls are transverse or only slightly oblique. The pits (fig. 4) are generally more or less oval-shaped and apparently simple, but whether an actual membrane separated one cell from the next in life cannot be determined. The pitting in some cells is more complex and may even approach reticulate banding. In certain of the more proximal sections in the series of peels taken through the specimen some of the cells of this tissue resemble the tracheidal cells of the traces. It is my suggestion that Darrah may have mistaken these for the second pair of traces mentioned in his account.

The abundant pitting of these cells and their great length as compared with the other non-vascular tissues suggest that their primary function was the conduction of fluids. In studying the seed from base to apex the presence of this tissue is first noted at the level of peel No. 7. From this point to approximately peel No. 11 it develops in abundance in two separate groups, sheathing the departing traces. The two groups soon expand in two C-shaped masses until they unite as a continuous band at the level of peel No. 29. The radial width of this band thereafter gradually increases as is shown in text-fig. 3.

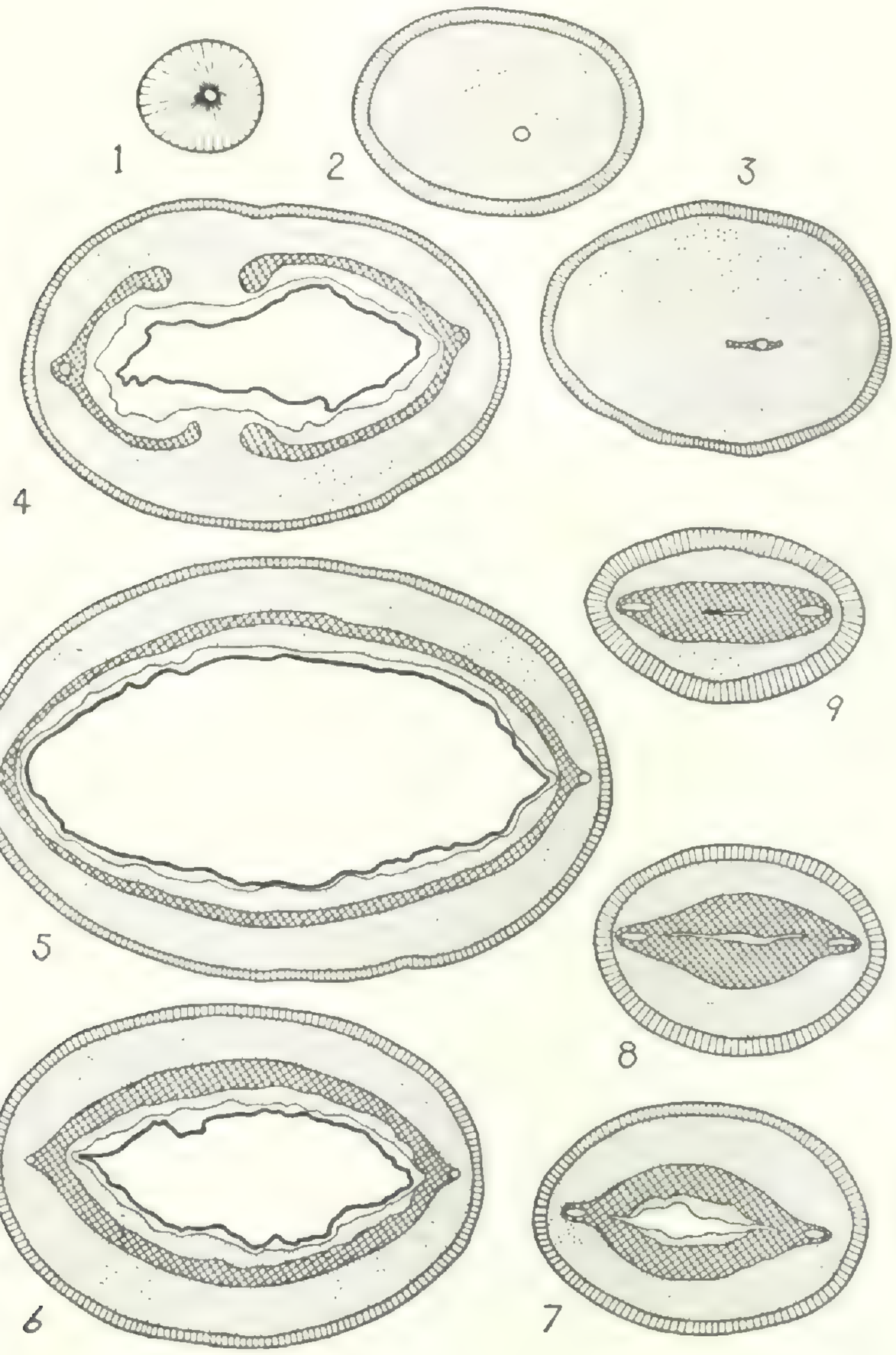
Within the sclerotic layer there is a fourth tissue consisting of very thin-walled cells which in most specimens has been lost through decay. In a few instances, however, it is possible to observe that this tissue did consist of rather thin-walled parenchymatous cells.

Within this fourth tissue layer it is possible, in most sections of the series, to follow a distinct, light yellow band around the periphery of the central cavity. The presence of this structure has been checked in numerous other specimens, and there seems to be no doubt that it is correctly identified as the megaspore membrane. Darrah has succeeded in isolating it very nicely by maceration, a fine illustration being given in his 1949 paper (fig. 11).

No tissue has been observed within this megaspore membrane. The shape of the internal cavity will, however, be described briefly. In following the series of transverse sections from proximal to distal end, at peel No. 10 a small cavity appeared in the position occupied in previous peels by the trace and its accompanying tissue. In peel No. 15 a similar cavity made its appearance on the opposite side and in peel No. 17 the two cavities merged. The fact that one cavity appeared before the other is due to a very slight obliquity in the internal structure of the seed, possibly a slight aberrancy of the particular specimen.

It thus appeared from a study of the serial sections that the internal cavity would be heart-shaped if viewed in median longitudinal section. It has been possible to confirm this supposition from such a nearly median section in the collections of the Harvard Botanical Museum. The basal portion of the specimen is

shown in figure 10. This is a trifle oblique to the median plane so that the actual entrance of the trace into the seed is not shown. The trace does appear, however, as a conspicuous mass of tracheids (fig. 10, t), flaring upwards and terminating the upper part of the cushion or "archesporial pad." A portion of one of the two traces is shown curving down and upward to the left in the outer parenchymatous tissue.



Text-fig. 3. A series of diagrams prepared from representative points in the series of transverse peels described on pages 480–484. 1, peel No. 1; 2, peel No. 3; 3, peel No. 8; 4, peel No. 20; 5, peel No. 38; 6, peel No. 53; 7, peel No. 64; 8, peel No. 66; 9, peel No. 69. Outer lined area, epidermis; stipple, outer parenchyma; cross-hatch, inner sclerotic tissue; inner stipple, inner parenchyma; heavy inner line, megaspore membrane. In 1 only the epidermis and central strand are shown; in 2 the epidermis, outer parenchyma, and central strand; in 3 the epidermis, outer parenchyma, central strand, and beginnings of the inner sclerotic tissue; 4–6 present the complete sequence of tissues with the traces shown at either end of the long transverse axis; 7 is taken above the distal limit of the megaspore.

Before leaving this description of the normal seeds I feel compelled to add a comment on Mr. Darrah's recent paper in which he sums up the distinctive features of these fossils: "Thus far in the development of the sporangium there are no structures or tissues which are unusual. Externally, there is the sporangium wall of usual lepidodendrid construction innermost the megaspore, which can be removed easily by maceration. The tissues between are sterile sporogenous tissues." (1949, p. 3). I do not understand the last sentence but to state that the sporangium wall with its thickness, its complex series of tissues, its vascularization, and its mode of attachment is "of usual lepidodendrid construction" certainly displays a taxonomic freedom that might allow the inclusion of anything within the genus *Lepidocarpon*. Darrah notes further that "My preference for broad rather than narrow interpretations of genera is well known." (p. 12). But surely somewhere there must be limitations.

I feel certain that there is nothing in the literature of lycopod sporangia, living or fossil, which presents a close comparison with this fossil. It is clearly far beyond the bounds of Scott's generic description for *Lepidocarpon* (Scott, 1901) and bears no resemblance to *L. lomaxi*, the type of the genus.

It is perhaps obvious that the principal problem that is involved in correctly interpreting the morphology of this fossil is whether we are dealing with a sporangium or whether it is a true seed. That is, whether the structure described above is a sporangium ("nucellus") enclosing a single fertile megaspore, or whether it is an integument enclosing the remains of a nucellus and the megaspore. I am of course following Darrah's interpretation in accepting the former choice. The reasons for this are as follows: There is no break in the continuity of the four tissues composing the wall of the fossil. They are all clearly in organic connection, there is no delimiting epidermal layer on the inside, and between this innermost parenchymatous layer and the megaspore there is no structure that might be interpreted as the remnants of a nucellus. Furthermore, there is no evidence that a micropylar opening existed at the distal end of the fossil. The tissue appears to be continuous here, allowing access of microspores only by a dehiscence of the sporangium, presumably along the lateral ridges.

Although the outer epidermal layer is very resistant, the shape of the cells and their alignment are as closely comparable to the prismatic epidermis of many cryptogamic sporangia as they are to the epidermis of seed integuments. It has long been recognized that the nucellus, in fact, is a modified sporangium and an epidermal layer so strongly suggestive of its sporangial homology is not surprising in a form that, as far as we know, probably lacks integuments completely.

The "proliferated" seeds.—

Associated with the above-described normal seeds in the Iowa coal balls from the Urbandale mine are other fossils of an even more problematical nature. I believe that they present, as Darrah indicates, a different growth stage than that of the normal specimens. It is freely admitted by the present writer that he is certain of neither their natural affinities nor their morphology but evidence will be

offered to support the contention that the structures described as "gametophytes" and "sporelings" are morphologically one and the same and that they constitute proliferations of sporangial wall tissue.

In the Urbandale coal balls that have passed through my hands some two or three dozens of these proliferated seeds have been observed but, as in the normal ones, a single particularly well-preserved specimen was selected for detailed consideration. However, casual study of the other less well-preserved ones clearly indicates that we are dealing with a typical specimen. In view of the unique nature of the fossils the reader is referred to figs. 18 and 19 as an aid in following the description. These are representative peels taken from specimen No. 519.

The over-all dimensions as illustrated in fig. 19 are 13 × 10 mm. Extending about half way around the specimen (the lower half as it is oriented in figs. 18 and 19) is an epidermis of heavily thickened palisade-like cells which, allowing for some variation among the individuals, agree exactly in size and shape with those of the epidermis of the normal seeds. Within this epidermis there is a parenchymatous tissue which composes the remainder of the fossil. This tissue consists of rather thin-walled cells; it is organically connected with the epidermis; it is vascularized; and it proliferates out into a central area in the form of branches of varying size. Each of these branches contains a delicate vascular strand and is bordered by a well-defined, thin-walled epidermis (fig. 13) which is consequently quite different from the outer epidermis of the fossil as a whole.

It does not seem necessary to comment on the outer thick-walled epidermal layer but a more detailed consideration of the parenchymatous tissue within is very much in order. This consists of rather irregularly shaped cells (fig. 3) in the peripheral region although in the central proliferating arms of tissue (fig. 13) the cells show some tendency to be elongated parallel to the long axis of the arms. It may be noted also in fig. 13 that the epidermis is only slightly differentiated from the interior parenchyma.

It is pertinent to indicate at this point the reasons for correlating these fossils with the previously described normal seeds. The former are, as noted above, somewhat larger and the epidermal layer is split and does not include the entire structure which would be expected if the normal seeds "germinated" to produce the distinctive proliferations shown in figs. 18 and 19. To me, it would seem most likely that the normal seeds or sporangia opened longitudinally along the ridged lateral edges. However, it has not been possible to determine the mechanics of germination from the available specimens, and I find it difficult to glean satisfactory information from Darrah's brief description of this point.

Like the epidermis in the two supposed growth forms, the outer parenchyma of the normal seeds agrees precisely with that of the proliferated seeds. It is clear that the parenchyma is in organic connection with the epidermis just as the epidermis and outer parenchyma of the normal seeds are organically connected, and it is equally clear, as shown in figs. 18 and 19, that there is no break in this parenchymatous tissue from the epidermis to the inner extremity of the arms. The

latter vary considerably in size, some being apparently simple unbranched structures while others branch rather profusely. In the specimen shown in figs. 18 and 19 there may be noted a rather massive central "clump" which gives rise to numerous branches. It will also be noted that many branches appear unconnected with the peripheral tissue but in following the series of peels many of these are readily observed to be connected and I believe that in view of the very close similarity of all of these central islands of tissue (as they appear in an individual peel) there is no reason to doubt that all are so connected. Finally it is important to note that all of these arms are vascularized by a delicate central strand of tracheids similar to those composing the traces of the normal seeds. Although the vascular strands of these are small and composed of few tracheids (fig. 14) the system as a whole is rather extensive. In fig. 18 a tracheidal strand may be noted at *t* and from this lateral strands branch out into the central arms.

Discussion.—

In the opening paragraph of his recent contribution Darrah states that "The discovery of well-preserved fossil embryos in a known plant group is therefore an event of considerable interest." There can be no doubt that such a discovery would be enthusiastically welcomed by botanists in general and paleobotanists in particular, and it is one that may be expected with justification due to the present interest in the coal-ball petrifactions. It is, however, my belief that satisfactory proof of this discovery has not been offered to date. It is not a pleasant task to have to refute the work of a colleague but in view of the seeming importance of these fossils no other course seems feasible. It is very possible that the restorations presented in Darrah's figs. 14–17 and fig. 45 (1949) might well be taken up by writers of text-books and without a first hand knowledge of the fossils it must be admitted that his descriptions are fairly convincing. It is my contention that these restorations showing "Lepidodendroid embryos" within the sporangia are entirely unjustified from the anatomical evidence, that the succession of tissues contained within the fossils has been misinterpreted, and that the evidence does not support the view that they are of lycopod affinities.

I wish to admit freely that satisfactory conclusions regarding the natural relationships of this fossil have not been reached yet. For nearly three years I have pondered over their morphology and affinities and have discussed them with numerous paleobotanists and morphologists. Sincere thanks are due to many of my colleagues for consoling suggestions. These fossils remain as the most problematical ones that I have had occasion to study, but in view of the above-mentioned publications it seemed necessary to present the results of my own observations to date. If future investigations are able to improve on the admittedly vague suggestions offered here they will be received cheerfully.

Darrah (1949) has interpreted the conspicuous peripheral parenchymatous tissue as a gametophyte and certain of the central patches of tissue as portions of

an embryo sporophyte. The basis for his differentiation of sporangial wall (or nucellar) tissue from gametophyte is not apparent in his illustrations or from his description. On page 3 he notes: "Close examination shows that a gametophyte has developed within the megaspore rupturing it and pressing it against the compressed sterile sporangial tissue (remnants of the megaspore membrane can in nearly all cases, be recognized)." And he also notes on this page that "The gametophyte is relatively undifferentiated." And on later pages reference is made to the "more or less disintegrated" gametophyte in more mature specimens in which the embryo sporophyte has developed at the expense of the nucellus and gametophyte.

Thus there is an essential conflict in our descriptions because my sections show clearly that the "gametophyte" and "nucellar" tissues are continuous and the same. Furthermore, no remnants of the megaspore membrane can be defined in any of the proliferated seeds I have examined.

In the well preserved specimen which serves as the basis for the present description there is no evidence of any disorganization of tissue in the peripheral region of the parenchyma adjacent to the epidermis. On the contrary, these two tissues are, as noted above, clearly in organic connection. The general organization and degree of maturity appear to be essentially identical with those described by Darrah. It will be helpful in this respect to compare figs. 18 and 19 with Darrah's figs. 3 and 4.

It would seem, therefore, that there is no justification for referring to a tissue organically connected with the epidermis of a sporangium as gametophyte and sporophyte. I can find no evidence for its alleged development within a megaspore wall. From the prominence of the yellow membrane in the normal seeds there is little question that it would be visible if it were present. It seems especially significant to note that in my specimen the peripheral tissue, that would be termed gametophyte in accordance with Darrah's interpretation, is clearly vascularized. There is no mention of such vascularization in his description, and this oversight may be, in part, responsible for the confusion.

In his fig. 6 Darrah shows what is claimed to be a megaspore membrane in the lower half of his seed and adds that "the tissue outside being in large part, if not entirely, sterile sporogenous tissue." (p. 7). This is a very critical point, and if it is "not entirely, sterile sporogenous tissue" (presumably this means tissue of the sporangium wall) some explanation of what it might be is certainly in order. In view of my own observations there also is doubt regarding the presence of a megaspore membrane in the section Darrah has illustrated. The definition of detail in Darrah's fig. 6 is so inadequate that the reader is afforded no basis for reliable interpretation, and the illustration in no way lends objective support to his conclusions.

Perhaps the most serious criticism that I find necessary to make is one pertaining to the reconstruction (fig. 45) of what is apparently a seed containing a

mature embryo. On page 7 Darrah notes four qualifications relative to this reconstruction. It is stated:

1. That the gametophyte is not shown since it would be more or less disintegrated. Yet no specimen is described in which this stage of development is in any way discernible.

2. That "the sporangium, with an embryo of this degree of development, would be ruptured, probably with the embryonic shoot considerably exserted." But the embryo is shown neatly curled within the unbroken sporangium epidermis.

3. That the "embryo would have a much greater number of leaves, particularly at the growing tip." But the description and illustrations in no way bear this out; and if there were many more leaves present it would seem that this point could have been readily shown in the drawing.

4. That "the orientation of the embryo is variable." I certainly agree that these parenchymatous proliferations are variable but it seems equally evident that they do not represent an embryo.

Following the enumeration of these four qualifications he concludes: "Nevertheless this sketch shows the zones of the embryo in their proper relation, and despite the rather unnatural aspect portrays the characteristics faithfully."

Accurate or even tentative paleobotanical restorations are certainly very much to be desired. Mr. Darrah deserves commendation for taking the trouble to summarize his findings in this form so that those who are not familiar with these fossils may gain a clearer concept of their life form, but to contend that the restoration "portrays the characteristics faithfully" seems to be very much at variance with the observable facts.

We may now return to the normal seeds to consider the supposed correlation of their contained tissues with those of the proliferated seeds. It is probably apparent that the most critical phase of this correlation lies in a determination of the origin of the parenchymatous tissue of the proliferated seeds. If Darrah's contentions are correct one would expect to find some remnants of the sporangial wall (nucellus) tissue, the megaspore membrane, and the gametophyte in those specimens containing immature embryos or even embryos in a rather advanced stage of development. Since no such sequence of disintegrated tissues is in evidence, and since tissues of the supposed gametophyte and sporeling are continuously traceable and connect with the sporangium wall epidermis, some other solution is necessary.

At this point it is pertinent to refer to the inner sclerotic layer of the normal seeds which is shown in figs. 12, 16, and 17. If Darrah's concepts are correct it is hardly possible that this tissue would have been completely disintegrated, yet he makes no mention of it in the germinating seeds. It is not clearly described in his 1941 paper (page 98) but the characteristic sclerenchyma is evident in the top figure of his plate II. No mention is made of the three dimensional aspect and pitting of these cells, so different from any other tissue in either the proliferated or normal seeds. My own observations on the elongate nature and pitting of these

cells were made largely on Darrah's own slides (preserved in the collections of the Harvard Botanical Museum) and it is difficult to understand why it is not given more prominence at least in the specific description, in view of the fact that, like the vascular strands, it is a tissue quite foreign to *Lepidocarpon*.

In his original paper (1941) on *L. glabrum*, following his discussion of the sporangium wall, Darrah notes that within this "The seed megaspore is always present" and in a later sentence adds "The gametophyte is extensive, nearly filling the whole cavity." No further description of the gametophyte is given nor do I find it possible to understand the caption to the lower figure of plate II (1941) in which the gametophyte is said to be present. One might overlook this lack on the assumption that the 1941 paper was a preliminary account but I do not feel that his description of the so-called gametophyte in the 1949 paper can be correlated with its organization as presented in the earlier contribution.

In view of the supplementary factual evidence presented here, the divergent descriptions, based, in part, on the same material, and the conclusion that this fossil cannot be referred to the genus *Lepidocarpon* the following emended diagnosis is given:

Nucellangium glabrum (Darrah) emend. Andrews.

Ovoid seed-like bodies approximately 12 mm. long and 6 × 9.5 mm. in diameter with a small circular hilum scar at proximal end. Presumably a sporangium with a wall consisting of the following sequence of tissues: a thick-walled, columnar epidermis; broad parenchymatous tissue of isodiametric cells; semi-sclerotic, longitudinally elongate, pitted cells; and a narrow thin-walled inner parenchyma. A single large megaspore contained within. Outer parenchyma traversed from base to apex by two delicate vascular strands.

The supposed proliferated form of the fossil somewhat larger, split longitudinally, consisting of the epidermis and outer parenchyma, the latter with numerous proliferating arms that extend approximately into the former area of the central cavity; peripheral region of this parenchyma as well as arms are vascularized.

Locality: Urbandale coal mine, Des Moines, Iowa, and other localities as given by W. C. Darrah, 1941.

Age: Middle Pennsylvanian, Des Moines series.

Specimens on which the present emended description is based are No. 677 and No. 519 in the paleobotanical collections of the Henry Shaw School of Botany.

In the previous accounts no specimens are specifically designated as the type or types. I have, therefore selected the following from Darrah's papers (1941, 1949) for this purpose: As the type for the normal seeds the specimen illustrated in the top figure of plate II (1941), No. 44103 in the collections of the Harvard Botanical Museum. As the type for the proliferated seeds the specimen illustrated in fig. 2 (1949).

Affinities of the fossil.—

I am keenly aware that the following remarks are inadequate as an explanation of the morphology and affinities of this fossil. It is quite evidently an instance in

which it is easier to destroy than to build, and if too much of the former has appeared in the preceding pages at the expense of a constructive treatment it is due partly to a lack of sufficient information and partly to an admittedly inadequate interpretation.

The suggestions that are given below are based, first, on the belief that *Nucellangium* is not a lycopod. At the expense of repetition the reasons for this belief may be briefly reviewed: The complex sporangium wall with its internal "sclerotic" conducting tissue, the vascularization, and the circular hilum scar. These seem to be of fundamental importance and are not in accord with previously described species of *Lepidocarpon*.

Upon the suggestions of at least two competent morphologists, which, incidentally, were offered independently, the possibility has been entertained that *Nucellangium* represents a hydropterid sporocarp. This possibility was supported by the general shape of the fossils, which is not unlike that of a *Marsilea* sporocarp, the mode of attachment, the thick-walled epidermal layer, and the vascularization of the peripheral parenchymatous tissue. However, certain features of the wall of the normal seeds, notably the inner sclerotic tissue and the single large megaspore, are not in accord with such a relationship, and the fertile specimens show no evidence of having borne sporangia after the manner of *Marsilea*. Furthermore, no associated remains are known which present hydropterid affinities. The possibility of such an affinity has, therefore, been abandoned.

Of the pteridophytic groups, other than the lycopods, which are known from the Upper Carboniferous there seem to be none which present a likely comparison. The remaining alternatives are the pteridosperms or cordaites as seed plant groups, or the possibility that we are dealing with an entirely distinct group of fossils, the affinities of which cannot be conjectured. Since the rest of the plant is not known, speculation in the latter direction at present seems useless. For reasons which will be given below it is, therefore, tentatively proposed that *Nucellangium* be considered as a primitive cordaite seed, or, if more noncommittal terminology seems preferable, a cordaite reproductive organ.

In searching for a lead that might suggest relationships with previously described fossils comparisons have been made with some of the many seed compressions. Of these, certain species assigned to the genus *Cardiocarpus* offer at least provocative suggestions. In examining the specimens of *Cardiocarpus* in the Lacoe Collection of the U. S. Geological Survey a few have been noted which correspond very closely to the expected appearance of a compression specimen of *Nucellangium*. For example *Cardiocarpus minor* Newberry (Lacoe coll., U. S. National Museum No. 25421) presents an aspect virtually identical with the profile of the broad face of the *Nucellangium* fossils. A compression of the latter would almost certainly produce a fossil that would be difficult or impossible to distinguish from this species of *Cardiocarpus*.

Although it is somewhat larger, *Cardiocarpus injens* Lesquereux (Lacoe coll., U. S. N. M. No. 25425) may also be mentioned since it displays an epidermal con-

figuration that compares closely with the type of epidermis of *Nucellangium*. *Cardiocarpus bicuspidatus* (Sternberg) Lesquereux, another compression species, also is closely comparable in size and shape with *Nucellangium*.

Since it may have some bearing on the present problem it seems significant to note that the many species assigned to *Cardiocarpus* (approximately 125 species are recorded in the U. S. Geological Survey's Compendium Index of Paleobotany) present an amazing variety of form. Were they better known I believe it is conservative to estimate that a few dozens of natural genera are included in this "compression dumping ground." For want of the necessary anatomical information that might allow a different disposition, these fossils are regarded as "seeds" and at present it seems most plausible that they have their alliance with plants of cordaitean affinities.

In tentatively considering the identity of *Nucellangium* with a species of *Cardiocarpus*, such as *C. minor*, a suggestion of the way in which they may have been borne is presented in Lesquereux's figure of *Cordaianthus spicatus* in the "Coal Flora" (Lesquereux, 1884, III, Pl. 109, fig. 1). Here are seeds of the *Cardiocarpus* type arranged pinnately in two rows on an elongate axis 5 mm. broad. A comparable organization is illustrated by Renault and Zeiller in their 'Flora of Commentry' (Renault and Zeiller, 1888) in figs. 30 and 31 of plate 73. Other authors have figured similar Cordaitalean inflorescences showing seeds of the *Cardiocarpus* type borne apparently terminally on the appendages of short branches. At this point it is perhaps significant to note that the most abundant plant remains in the coal balls from which *Nucellangium* has been obtained are the inflorescences, stems, and leaves of the cordaitales. I am aware that the evidence afforded by association is hardly conclusive, yet in view of the abundance of these cordaitean remains, and the *Nucellangium* fossils which compare closely with compressions known to have been borne on *Cordaianthus* inflorescences, some significance may be attached to this association.

In attempting to postulate a satisfactory explanation of the morphology and affinities of *Nucellangium* it is clear that the unintegumented nature of the fossil is particularly perplexing. I feel quite certain that the normal seeds as described in the earlier portion of this paper represent a nucellus or sporangium wall and in this one respect I seem to be in accord with Mr. Darrah. Is it plausible that we are dealing with an aberrant cordaitean stock whose presence has not been previously suspected? The possibility may exist, of course, as Darrah suggested, that the seeds were shed from their integuments but at present there appears utterly no evidence that would serve even for conjecture.

It is clear that we are dealing with a sporangium possessing a wall that is specialized as a protective device to a very high degree. Certainly the epidermal layer would have served most effectively against the attacks of fungi or small animals and equally well to prevent the loss of water from within. Can it be that we are dealing with a plant in which this protective function of the integument was developed by the sporangium wall, that is, the tissue that would normally have evolved into a nucellus of the more usual type?

With reference to the morphology of the proliferated seeds the problem becomes much more involved. Having discarded the gametophyte-sporeling nature of these bodies some other explanation is clearly in order. It is tentatively suggested that the proliferated specimens could represent either aposporus growths of the outer parenchymatous layer of the nucellus, or a gemma-type reproductive tissue. If any weight can be placed on the suggestion that the proliferations represent an aposporus tissue it would seem likely that archegonia should be found in some abundance, but none have been observed in the specimen described here. It is, moreover, strange that sporelings, as described by Darrah, are so abundant and yet no trace of their earlier stages is present, and only one archegonium has been reported.

The fact that the parenchymatous tissues of the proliferated specimen, both the peripheral region and the internal "arms," are vascularized, is indicative of sporophytic rather than gametophytic tissue. It would seem, therefore, that the most likely function this structure served was as a purely vegetative reproductive organ—that is, a gemma in the broad sense. It is assumed, following this interpretation, that the proliferations developed directly into a new sporophyte plant. Such being the case, it seems likely that the central proliferated "clump" shown in figs. 18 and 19 represents the initial apical meristematic region of the new sporophyte.

The question of course will arise as to the disappearance of the inner sclerotic layer which is so conspicuous in the normal seeds and the only explanation that I am able to offer is that the characteristic development of the proliferated seeds originated before the normal maturation of the internal tissue layers.

Acknowledgment.—

The abundant Urbandale coal balls, containing a wealth of well preserved, unique plants have been gathered by Mr. Frederick O. Thompson of Des Moines. Unfortunately it has not been possible to obtain more of this material in recent years and although we may reasonably hope that other Iowa localities will eventually contribute toward a more satisfactory solution of this and other paleobotanical problems there appears to be little chance of obtaining more Urbandale coal balls. It is partly on this account that the present writer has decided to submit his study of the available specimens of the fossil described above.

It is a pleasure to acknowledge again with gratitude the contributions that Mr. Thompson has made in aid of our investigations of American Carboniferous plants.

Sincere thanks are also due Dr. James M. Schopf for his many helpful suggestions during various stages of this study. The author, however, assumes all responsibility for such criticism, theories, and conclusions as may be found herein.

Bibliography.—

Andrews, H. N. and Jules Kernen (1946). Contributions to our knowledge of American Carboniferous floras. VIII. Another *Medullosa* from Iowa. Ann. Mo. Bot. Gard. **33**:141–147.

Darrah, W. C. (1941). The fossil flora of Iowa coal balls. IV. *Lepidocarpon*. Harv. Univ. Bot. Mus. Leafl **9**:85–100.

———, (1949). Paleobotanical Notices II. Paleozoic Lepidodendroid embryos. Medford, Mass. published by the author.

Lesquereux, L. (1884). Coal flora of the Carboniferous formation. 2nd Geol. Surv. of Penna.

Renault, B. and R. Zeiller (1888). Études sur le terrain houiller de Commentry, Atlas. Soc. del 'Industr. Min., St. Etienne.

Scott, D. H. (1901). On the structure and affinities of fossil plants from the Palaeozoic rocks. IV. The seed-like fructification of *Lepidocarpon*, a genus of lycopodiaceous cones from the Carboniferous formation. Phil. Trans. Roy. Soc. Lond. **194**:291–333.

Explanation of Plate

PLATE 35

Note: A considerable number of the following figures are taken from the series of peels described on pages 481–485. The peel number refers to the respective position as indicated in text-fig. 1. The slide number is the permanent one assigned in the paleobotanical slide collection of the Henry Shaw School of Botany.

Nucellangium glabrum

Figs. 1, 2. Specimens isolated whole from coal balls. The one in fig. 1 displays the hilum scar at the base; this specimen was used in preparing the series of peels described on pages 481–485. × 5.

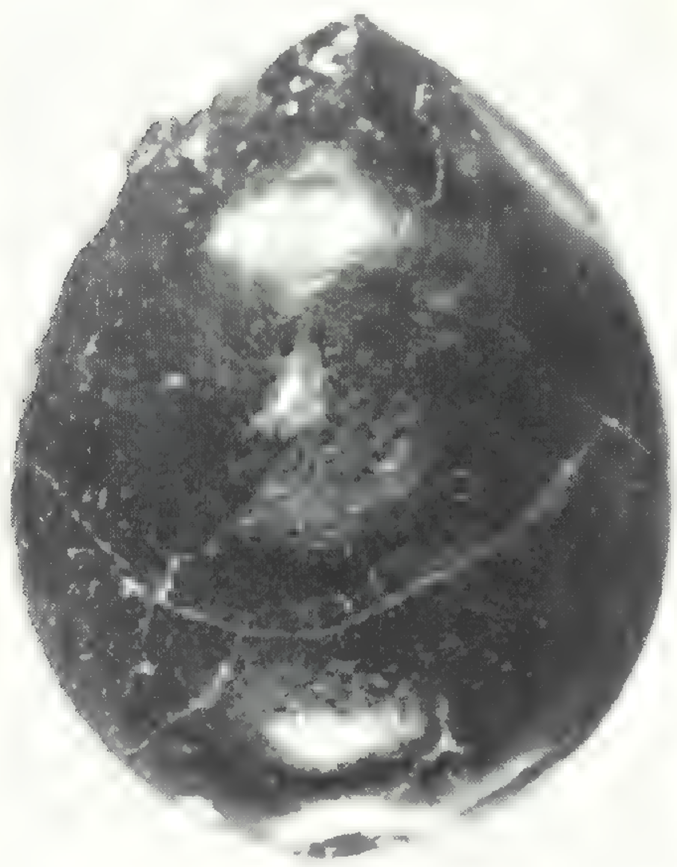
Fig. 3. Epidermis and outer parenchyma showing the two in organic connection in a proliferated seed. Slide No. 1497. × 85.

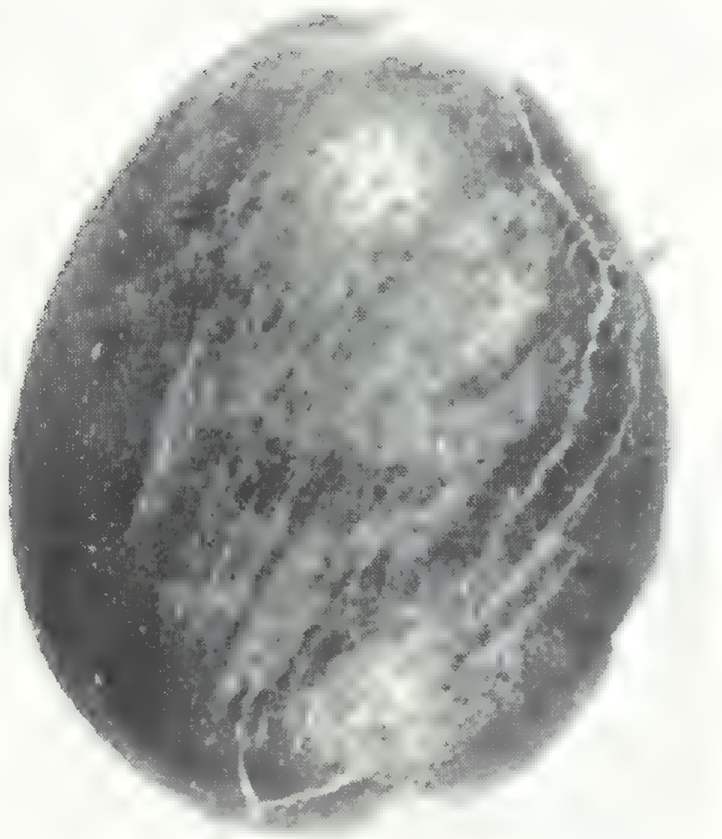
Fig. 4. Cells, showing pitting, of the inner sclerotic tissue of a sterile seed in longitudinal view. From slide No. 50896, collections of the Botanical Museum of Harvard University. × 225.

Fig. 5. Hilum scar of the specimen shown in fig. 1. × 20.

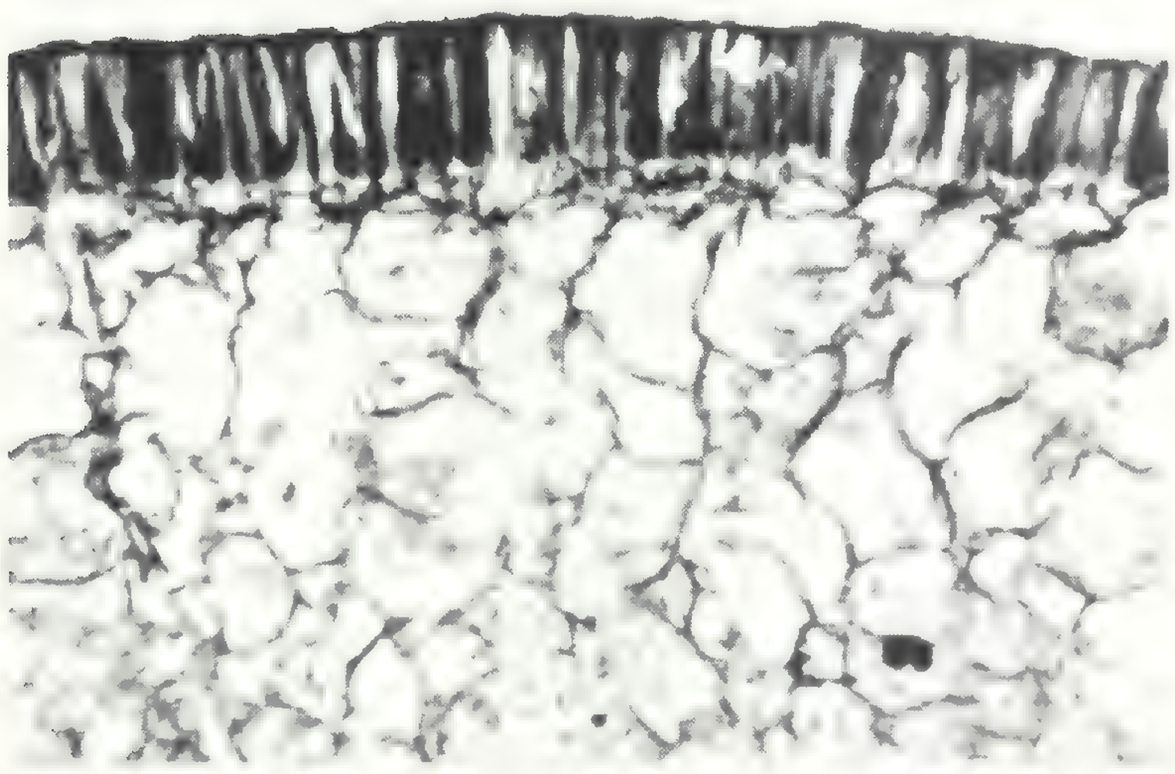
Fig. 6. Photograph of peel No. 9 (slide No. 1643) showing central vascular strand (near base of seed) in right center, and departing trace at left. × 110.

1



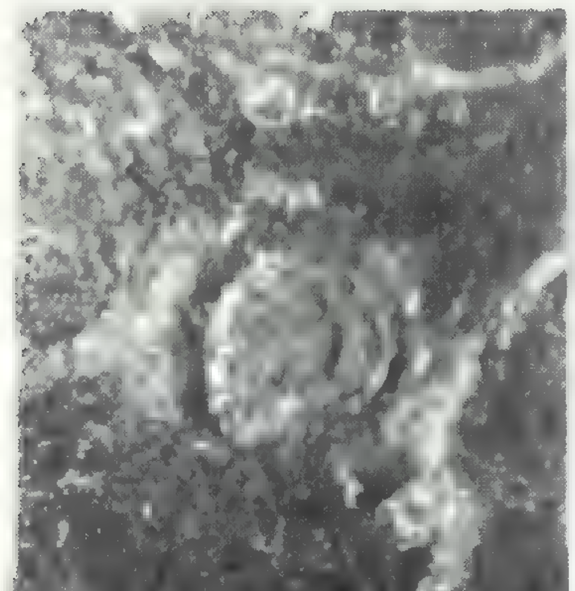


2



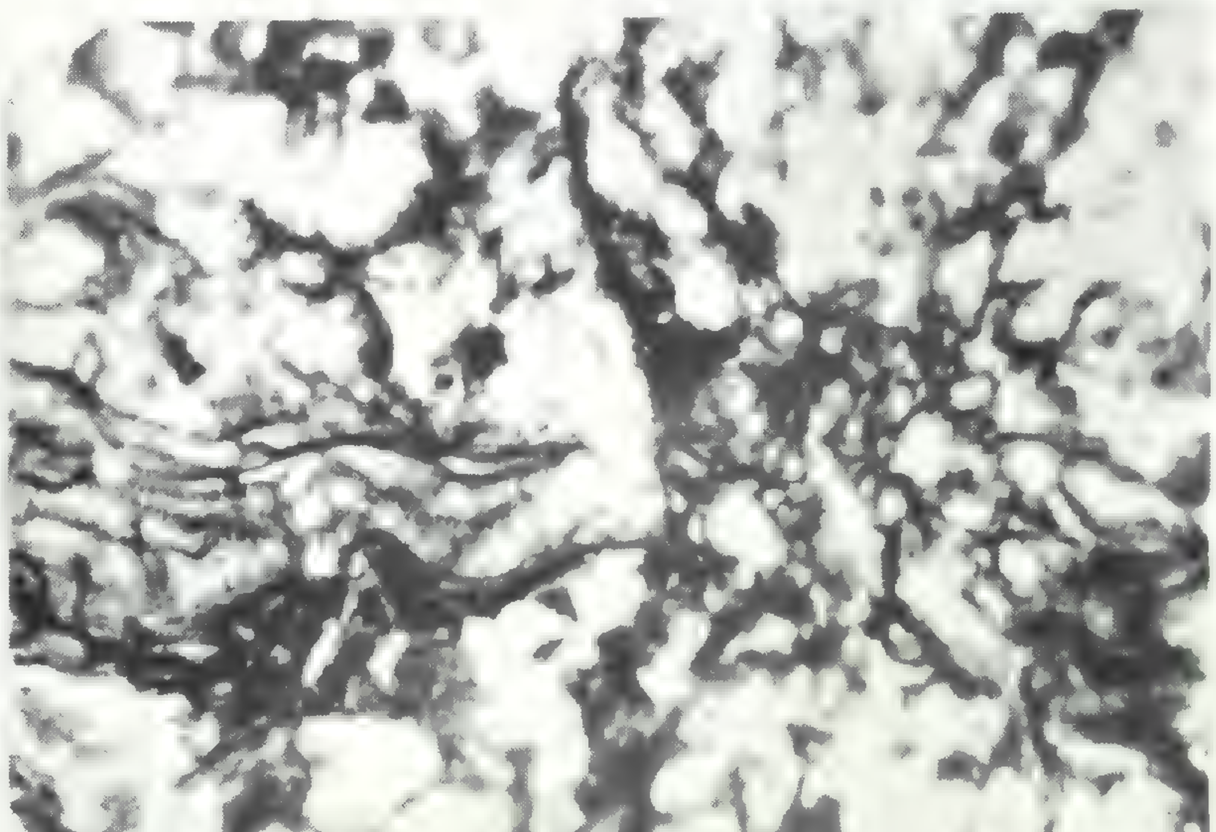
3

4



5

6



Explanation of Plate

PLATE 36

Nucellangium glabrum

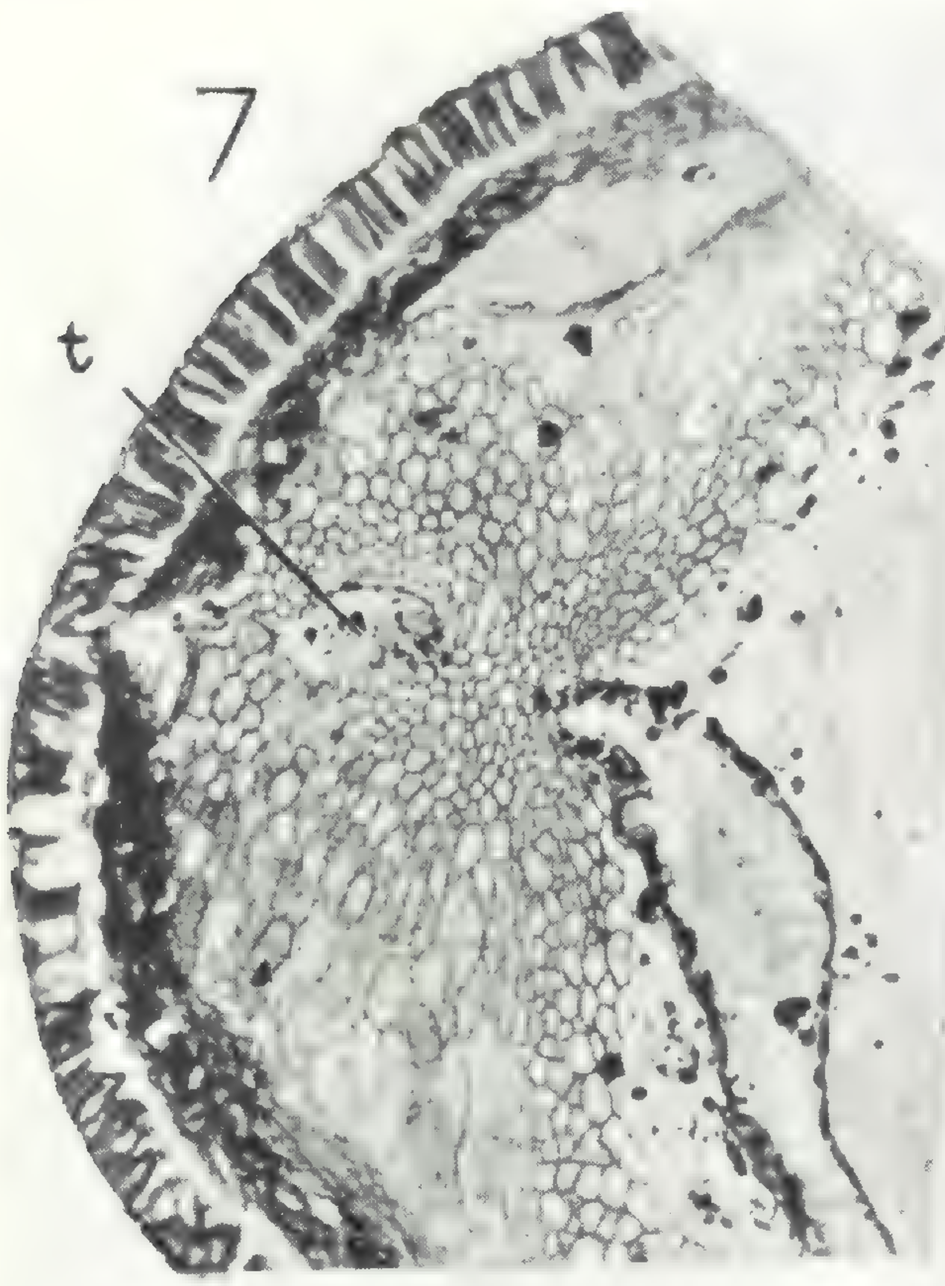
Fig. 7. Part of transverse section through the median region of a seed showing the vascular trace on that side. From slide No. 50897, collections of the Botanical Museum of Harvard University. × 54.

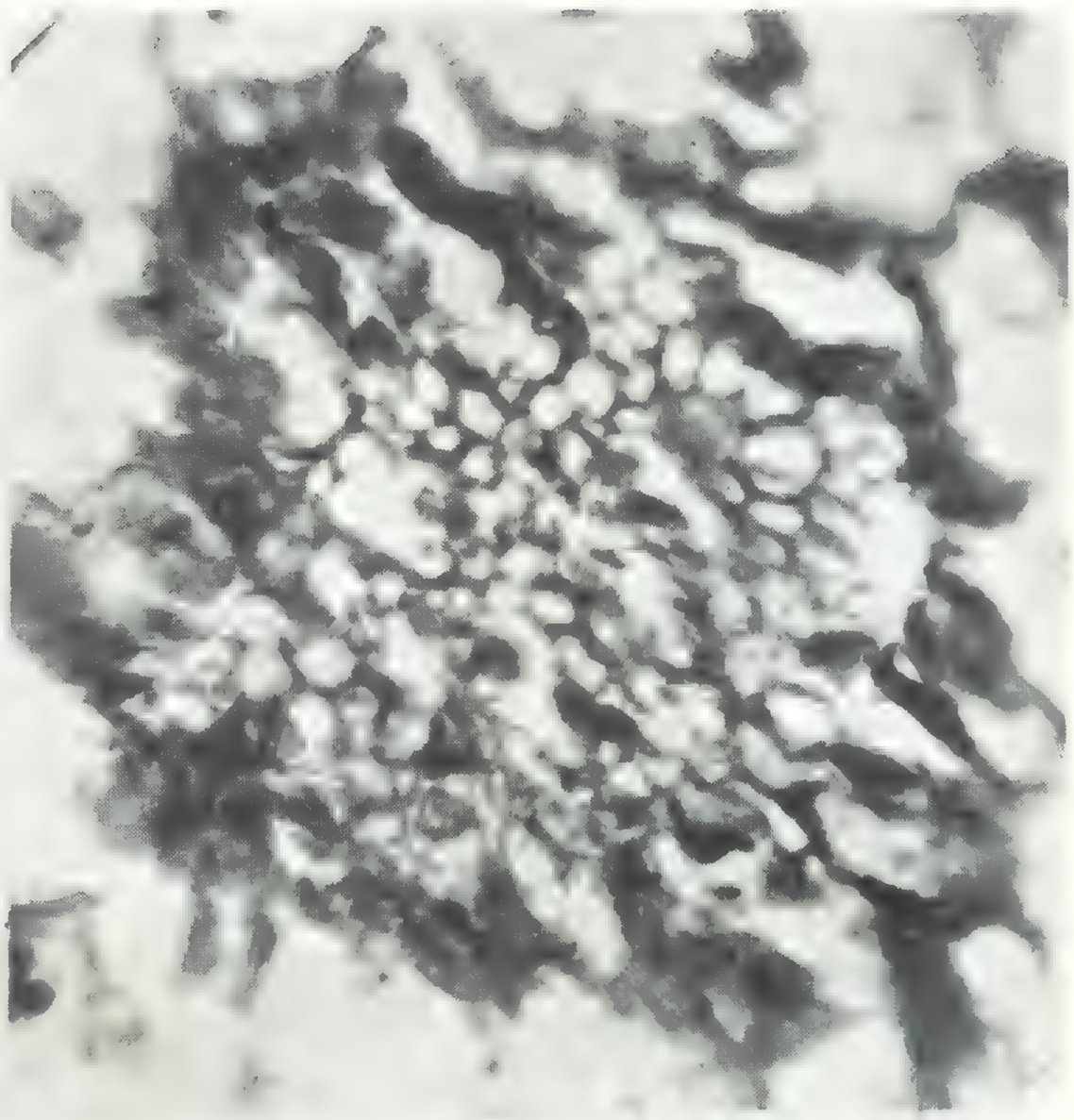
Fig. 8. The central vascular strand in the base of the seed, from peel No. 13 (slide No. 1647). × 220.

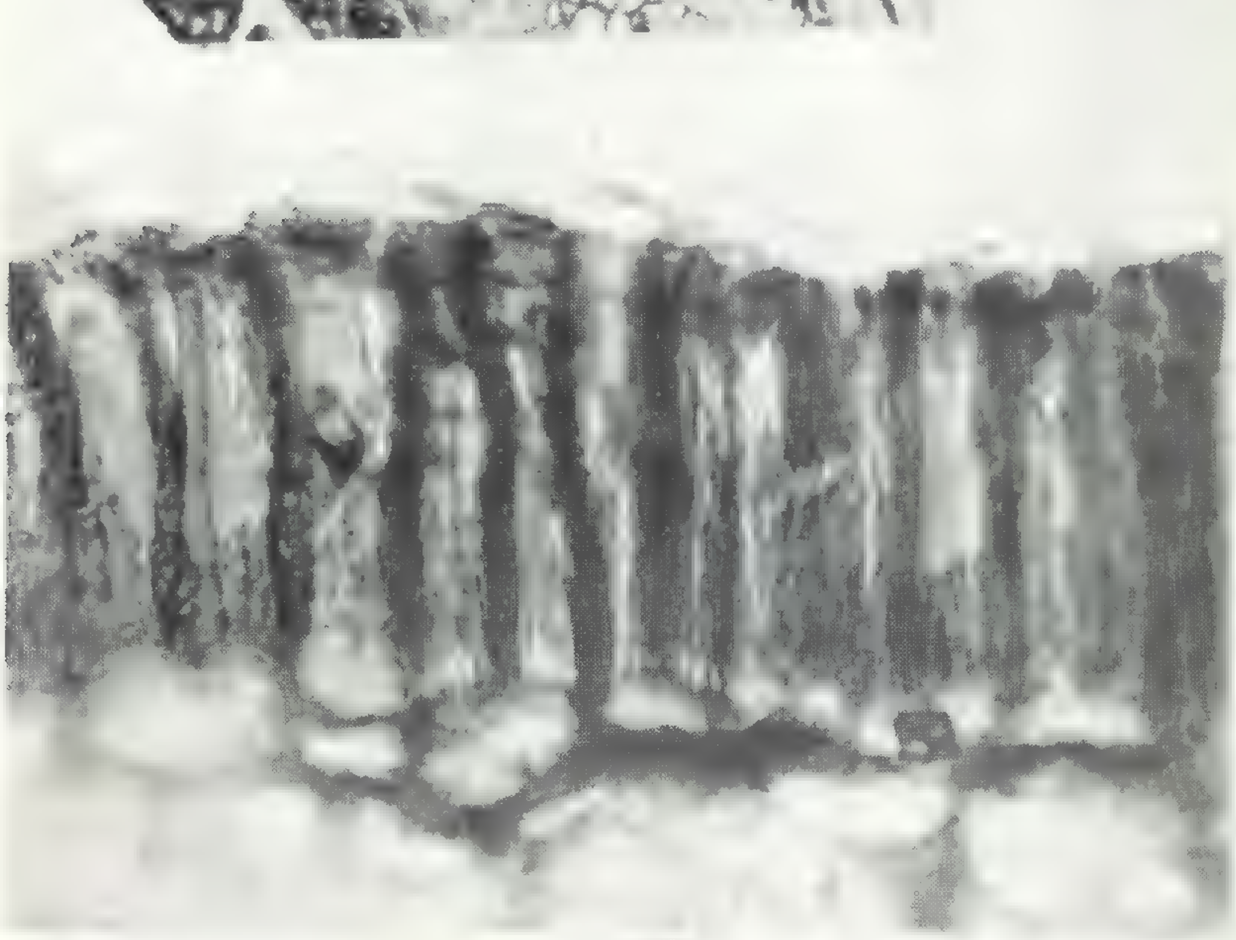
Fig. 9. Section through epidermis of normal seed, from peel No. 34 (slide No. 1656). × 280.

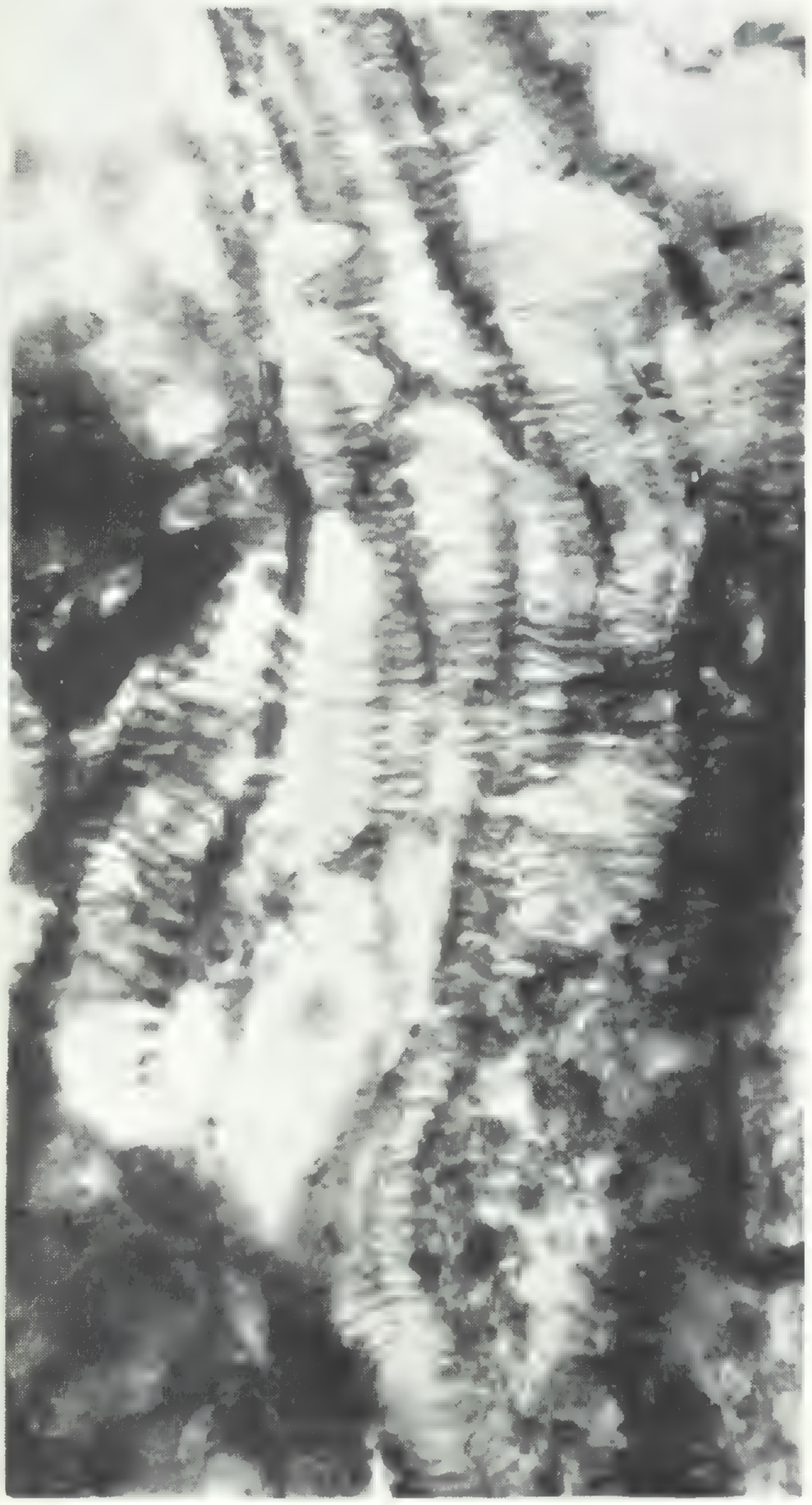
Fig. 10. A nearly median longitudinal section through the basal portion of a seed. *t*, tracheidal tissue in "archesporial pad." From slide No. 50895, collections of the Botanical Museum of Harvard University. × 16.

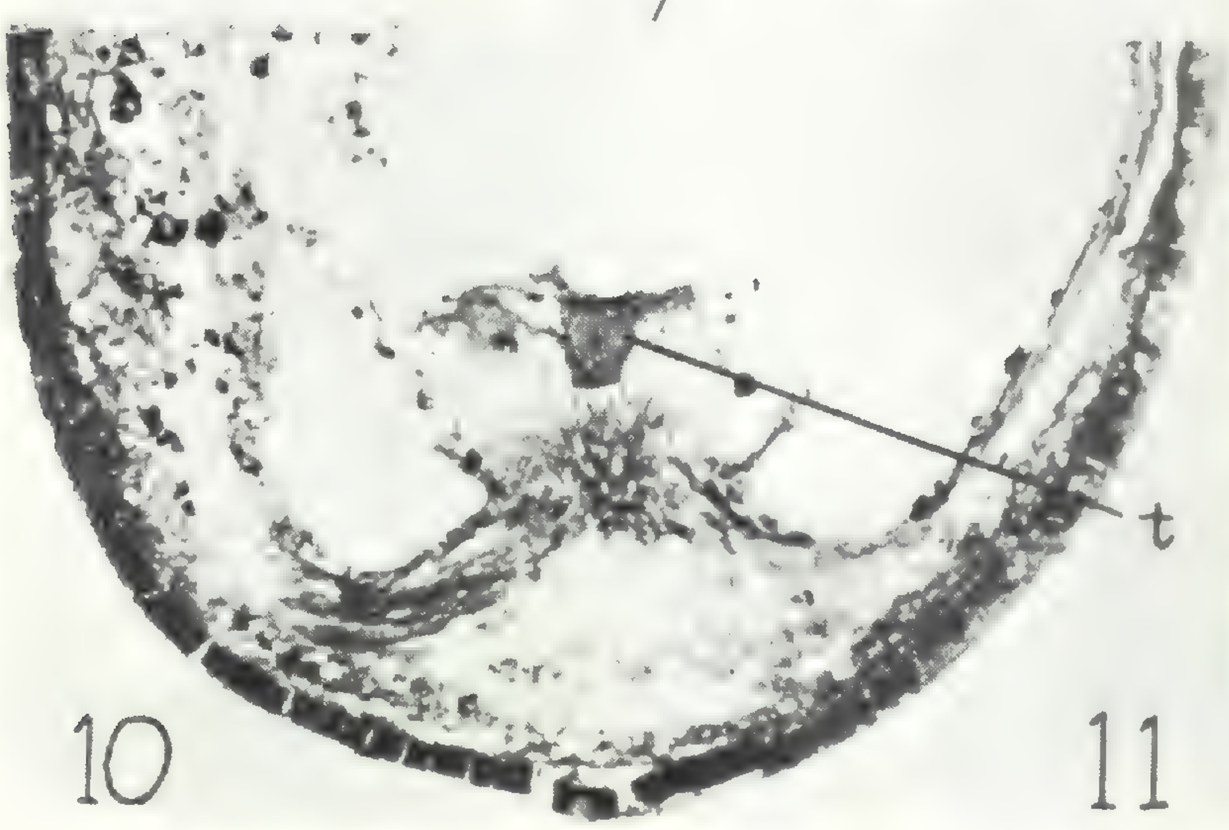
Fig. 11. A highly magnified view of a branch trace of the normal seed, from peel No. 8 (slide No. 1642). × 500.


7
t


8


9




t
10

11

Explanation of Plate

PLATE 37

Nucellangium glabrum

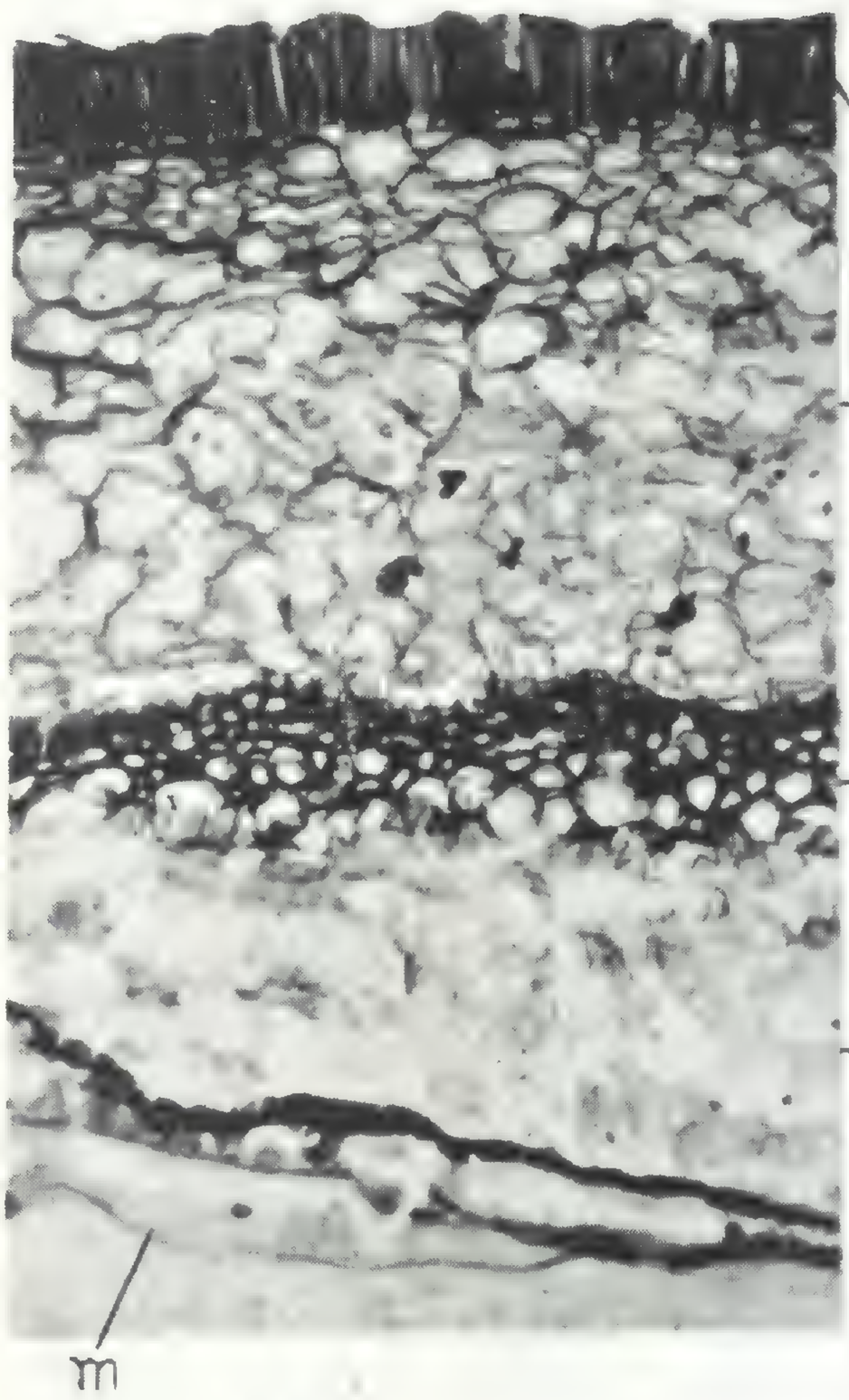
Fig. 12. Transverse section through the wall of the normal seed, from peel No. 34 (slide No. 1656): *e*, epidermis; *op*, outer parenchyma; *is*, inner sclerotic layer; *ip*, inner parenchyma; *m*, megaspore membrane. × 65.

Fig. 13. One of the central arms, or branch proliferations, from the specimen in fig. 18. Slide No. 1496. × 80.

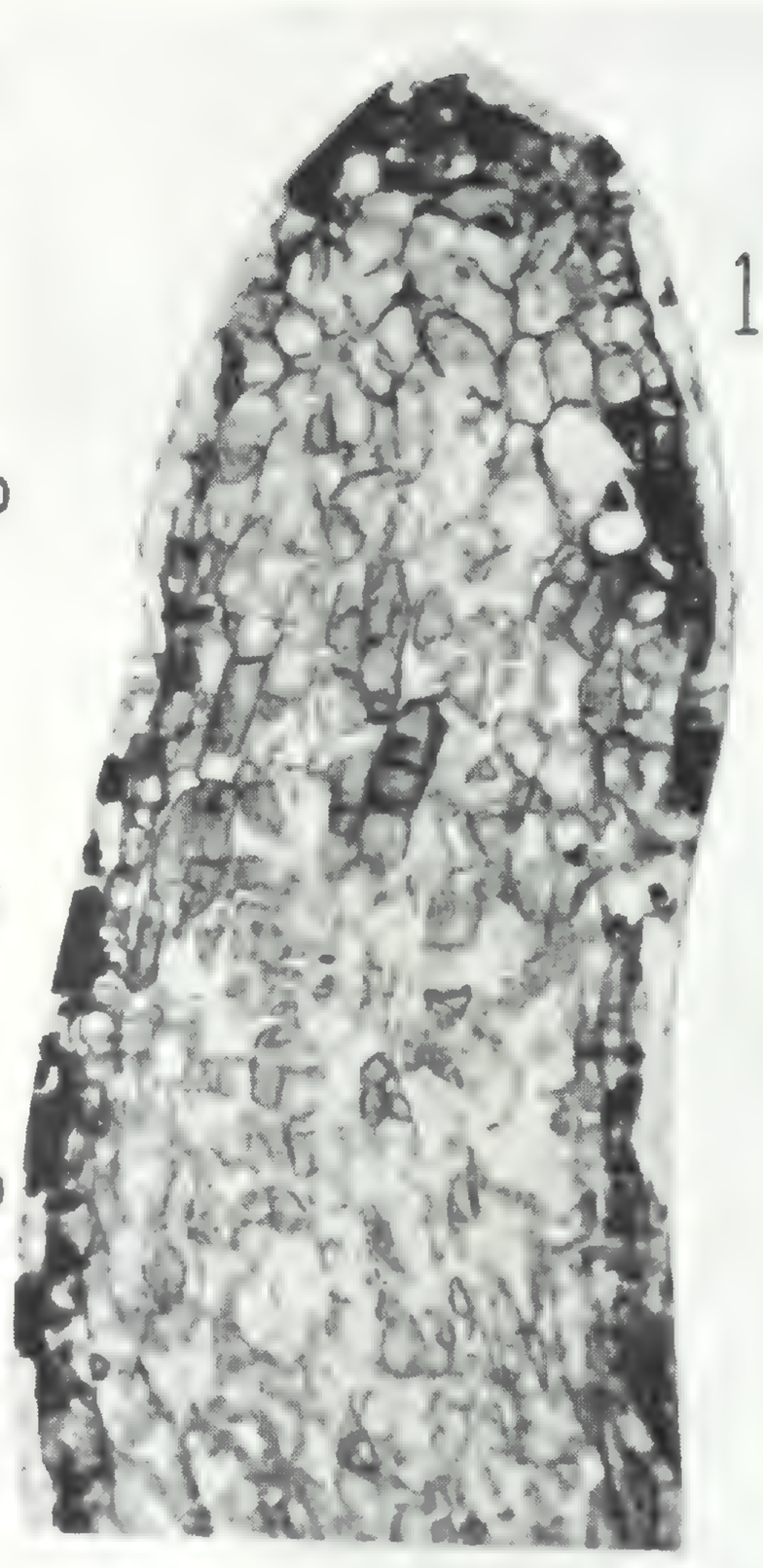
Fig. 14. A vascular strand of the proliferated specimen (fig. 18). Slide No. 1498. × 440.

Fig. 15. A section in the transverse plane through a normal seed taken at one side of the central basal strand. The dark tissue represents the lowermost extension of the inner sclerotic tissue. This is associated at this level with the departing traces and is shown in text-fig. 3 (3) as the small central cross-hatched areas. From peel No. 11 (slide No. 1645). × 80.

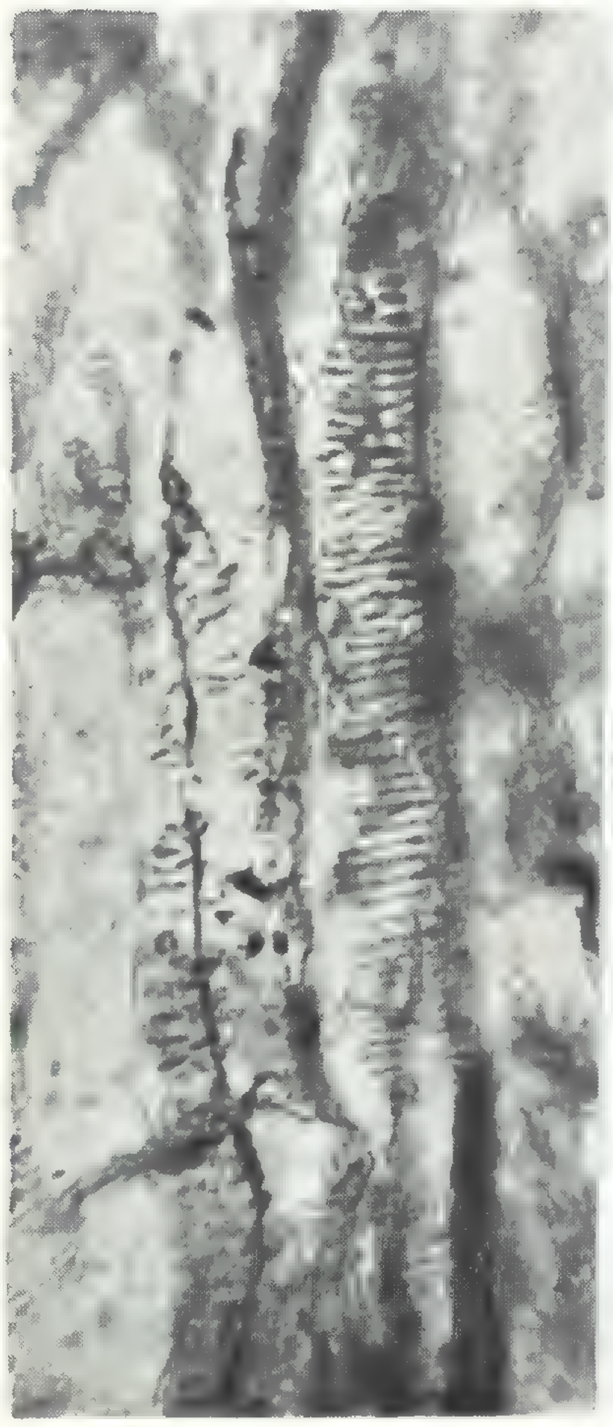
12



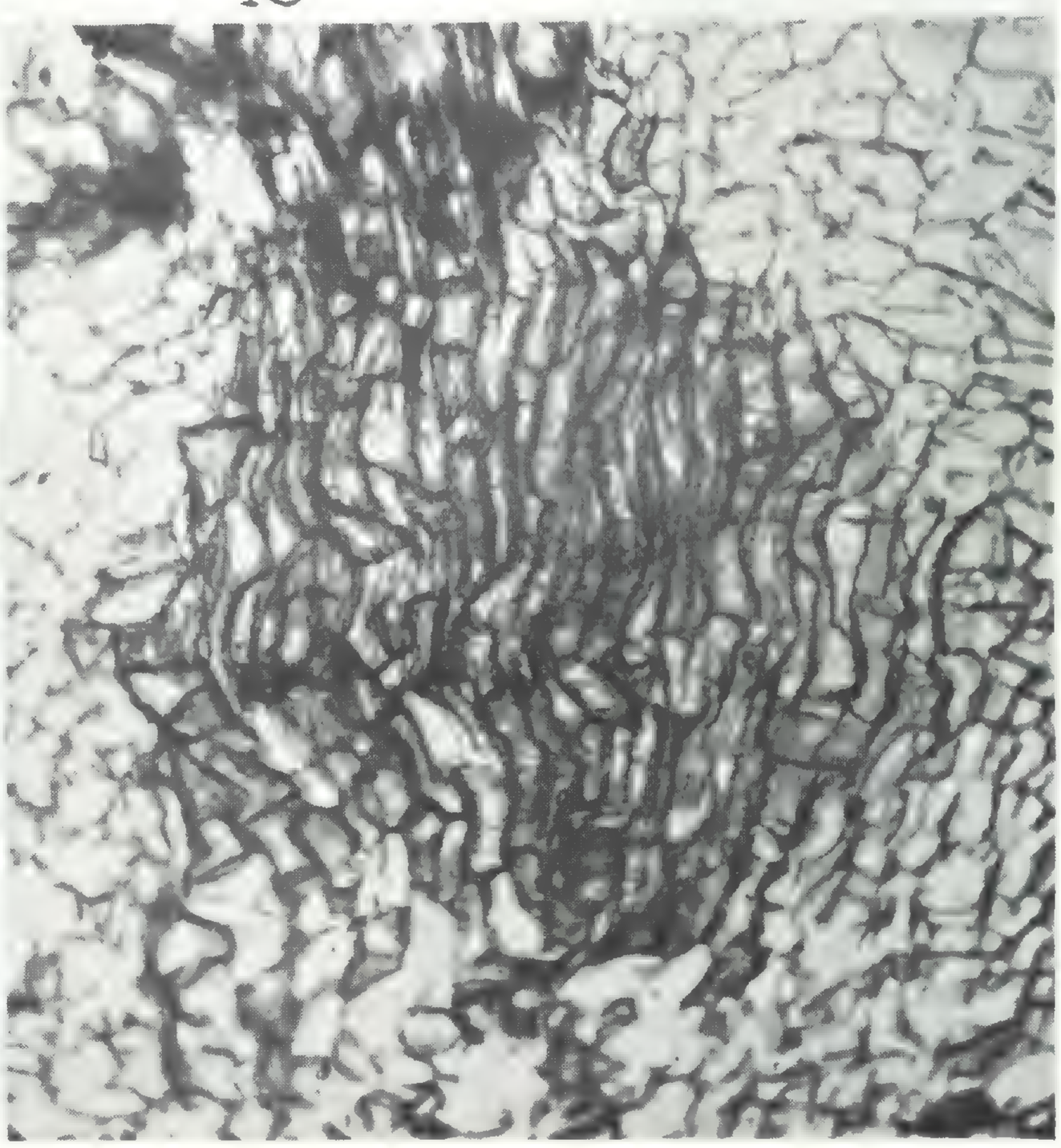
13



14



15



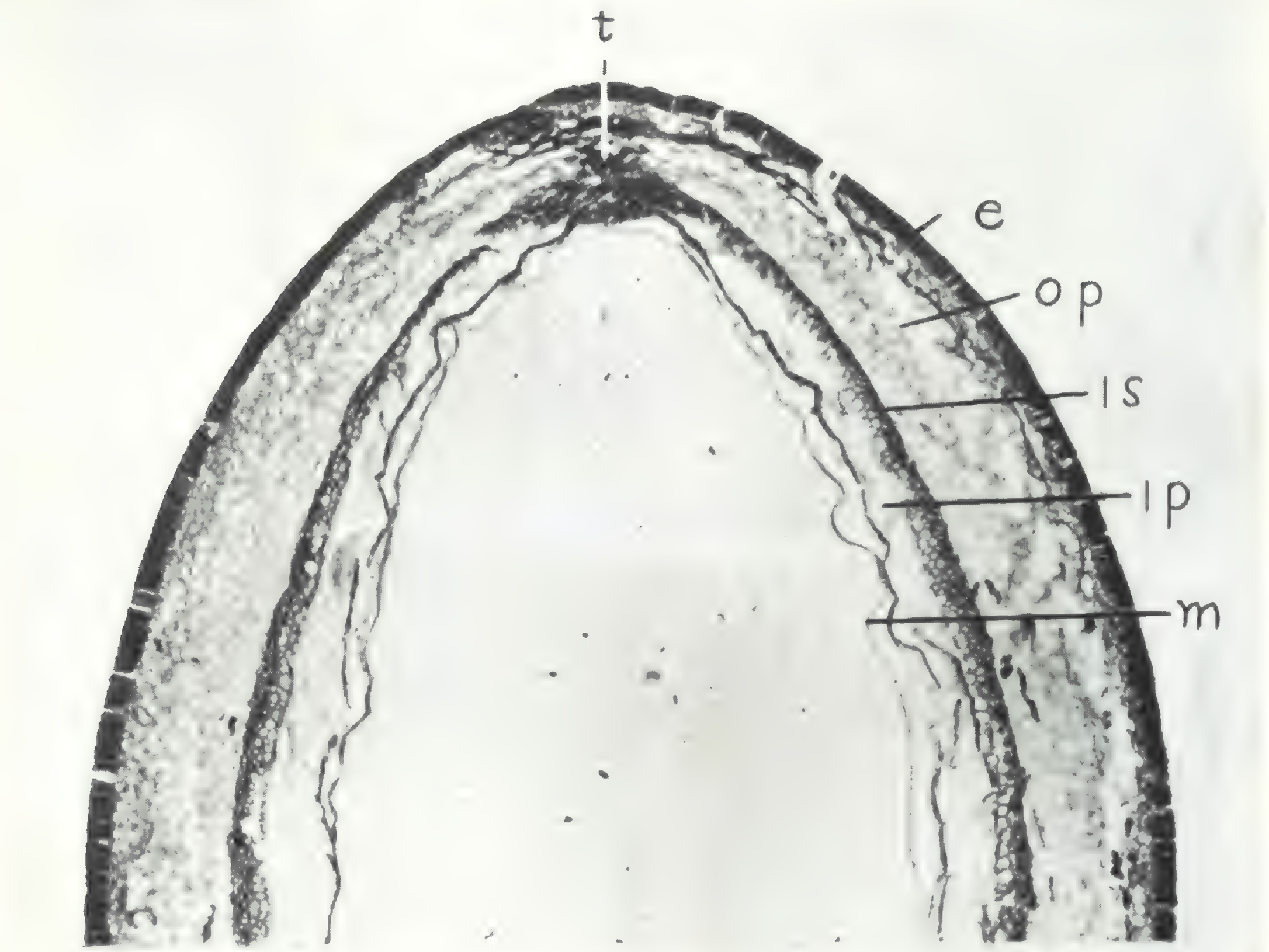
Explanation of Plate

PLATE 38

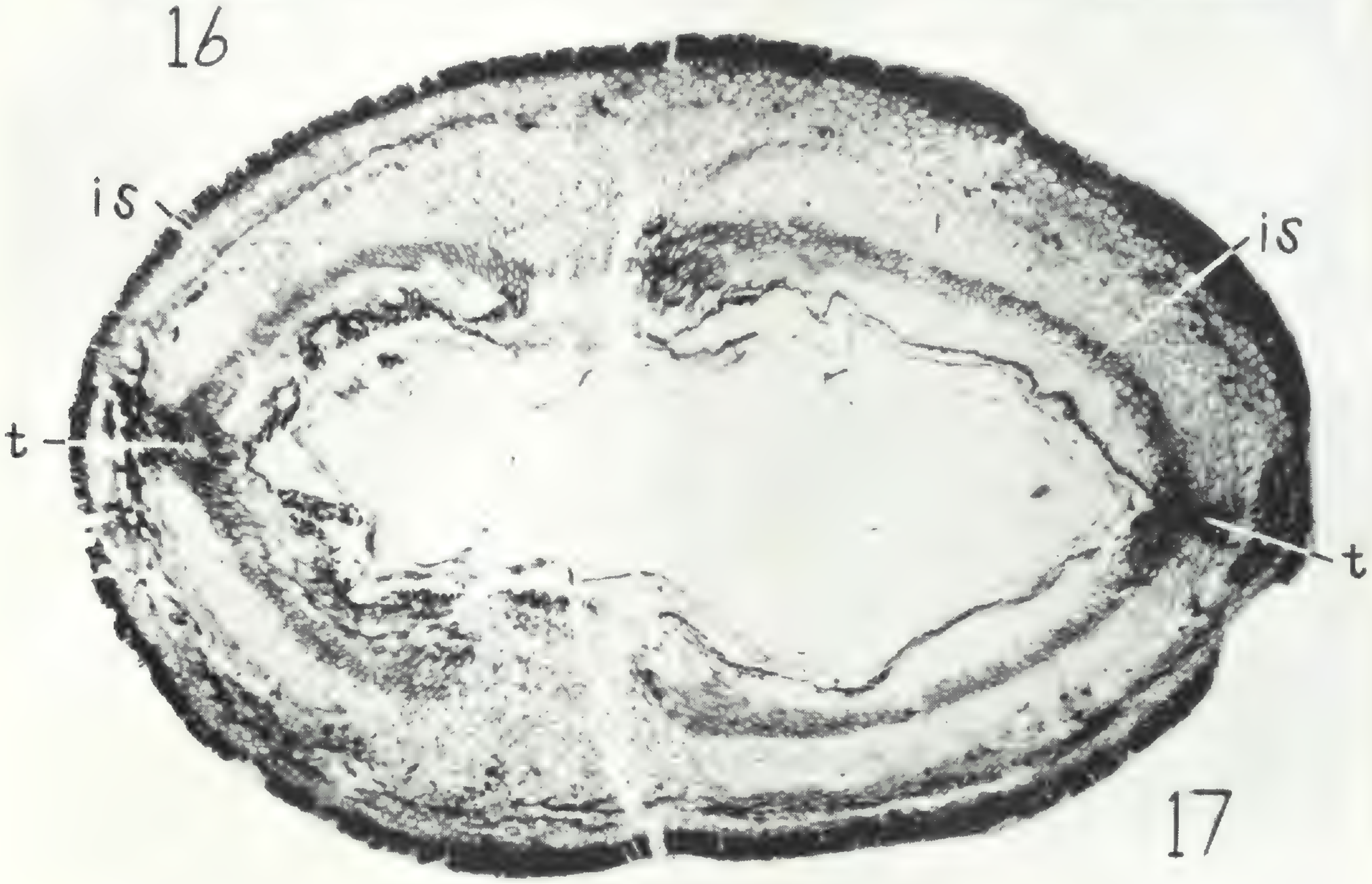
Nucellangium glabrum

Fig. 16. Photograph showing half of the transverse section of the normal seed, peel No. 38 (slide No. 1658): *e*, epidermis; *op*, outer parenchyma; *is*, inner sclerotic layer; *ip*, inner parenchyma; *m*, megaspore membrane; *t*, vascular trace. × 20.

Fig. 17. Complete transverse section of the normal seed, peel No. 20 (slide No. 1653): *t*, position of traces; *is*, inner sclerotic layer Note interruptions of the inner sclerotic layer on the two sides; compare with text-fig. 3 (4). × 18.



16



17

EXPLANATION OF PLATE

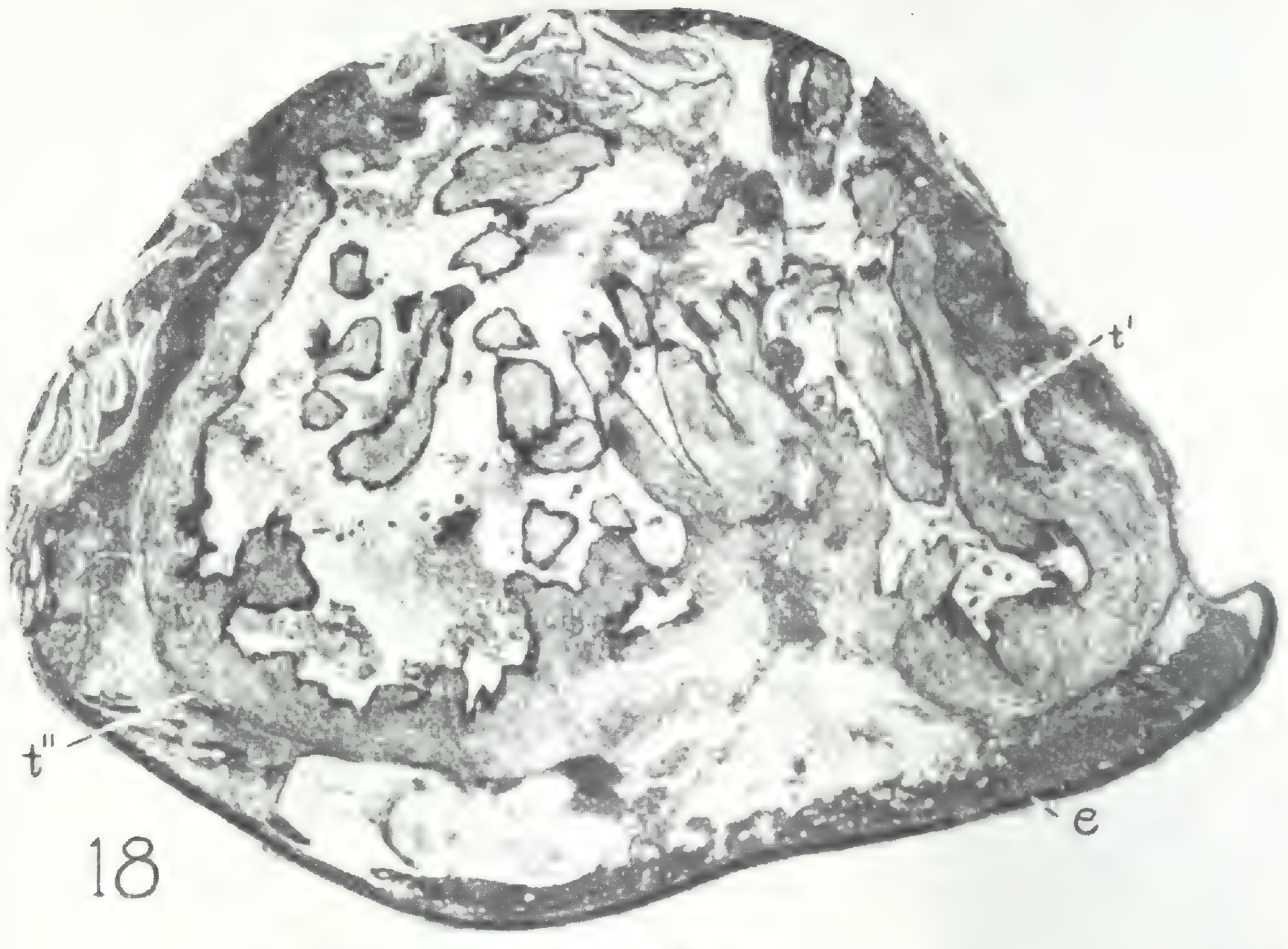
PLATE 39

Nucellangium glabrum

Figs. 18, 19. Photographs of sections of the proliferated specimen described on pages 486–488.

Fig. 18. From peel No. 519.T7 (slide No. 1674): *t'*, vascular strand in proliferated arm (see fig. 14); *t''*, vascular strand in peripheral parenchymatous zone; *e*, epidermis. × 12.

Fig. 19. From peel No. 519.T29 (slide No. 1675): *e*, epidermis; *p*, peripheral parenchymatous zone which is in organic connection with the epidermis (*e*), and from which the proliferated arms arise; *i*, by following through successive peels these scattered "islands" of tissue may be observed to be proliferated from the peripheral parenchyma zone. × 16.



18

19

A REVISION OF THE GENUS HELIOCARPUS L.[1]

KO KO LAY

INTRODUCTION

Heliocarpus has received considerable attention from plant systematists probably because of the perplexing variation found in the genus and because of the few constant characters of taxonomic value. Furthermore, in the herbarium, the specimens are either in fruit or in flower, never both; and when in flower are either hermaphrodite or pistillate. Thus, assigning them to any particular species becomes extremely difficult. Despite a recent taxonomic study of the genus,[2] there is still considerable confusion regarding many species both in the literature and in the herbarium. More than fifty species and varieties have been named thus far, and with the prevalent vagueness in the concept of speciation, there appears superficially to be but two alternatives: either to split the genus into innumerable indistinct and undefinable "species" or to lump them indiscriminately into few categories of scarcely greater reality.

In my study of the genus an attempt has been made to escape this dilemma by clarifying the concept of speciation. However, as this study has been confined entirely to herbarium specimens which represent only very small portions of the woody plants, no definite idea or suggestion as to the individual variations of single plants has been obtained. I have been fortunate enough in being able to study specimens from nearly all the major herbaria both in the United States and in Europe. The standard method of the herbarium taxonomist has been used for the interpretation of the species, and an attempt has been made to identify the fruiting specimens with the flowering ones. As far as possible, no intergrading forms have been considered as worthy of specific rank, and I have tried to group the "species" into fewer categories of perhaps greater biological reality, in the hope that they will be satisfactory both from a taxonomic and from a practical standpoint. The key has been so prepared that it should be usable for both the fruiting and the flowering specimens.

GENERIC RELATIONSHIPS

Heliocarpus L.[3] commonly is referred to the tribe Grewieae[4] of the family Tiliaceae and usually is recognized by its characteristic fruits. The genus is distinct from the other genera of Grewieae except *Triumfetta*. There is no difficulty in distinguishing the two genera when both are in fruit, as the fruits are very dis-

---

[1] An investigation carried out at the Missouri Botanical Garden and submitted as a thesis in partial fulfillment of the requirements for the degree of Master of Arts in the Henry Shaw School of Botany of Washington University.

[2] Watson, E. E. The genus Heliocarpus. Bull. Torrey Bot. Club 50:109. 1923.

[3] Sp. Pl. ed. 1. 448. 1753.

[4] K. Sch. in Engl. & Prantl, Nat. Pflanzenfam. III[6]:29. 1895.

tinct. A very good description of the fruit of *Heliocarpus* was given by Linnaeus[5], who asked, in naming the genus, "Who could ever behold an almost rounded fruit, bordered with a halo of rays, without thinking of the sun as conceived by the painters?" In *Triumfetta* the fruit is a burr, with many bristles all over the surface.

It is slightly more difficult to differentiate between the two genera in the case of flowering specimens. Both have alternate, palmately reticulated leaves with long, slender petioles and stellate pubescence. The aspect of the specimens also is very similar and the superficial resemblance rather striking. The chief differentiating characters may be summarized as follows:

(1) *The inflorescence*—In *Heliocarpus* usually terminal, and when axillary large and spreading; in *Triumfetta* generally axillary, rarely large and spreading.

(2) *The cymes*—In *Heliocarpus* disposed in nodose clusters of about 12–20 flowers each; in *Triumfetta* generally not in nodose clusters, and if in nodose clusters usually 6- to 12-flowered.

(3) *The flowering peduncles*—In *Heliocarpus* nearly always 3-flowered (rarely 2-flowered), and usually ebracteolate; in *Triumfetta* 1- or 2-flowered (rarely 3-flowered) and conspicuously bracteolate.

(4) *The mature floral buds*—In *Heliocarpus* as long as 6–7 mm., the sepals appendaged or unappendaged at the tips, the petals valvate; in *Triumfetta* as long as 2–3 cm., the sepals always with apical appendages, the petals with twisted aestivation.

(5) *The number of stamens*—In *Heliocarpus* usually 12–40; in *Triumfetta* usually more numerous.

(6) *The gonophore*—Simple in *Heliocarpus;* in *Triumfetta* with a ciliate saucer-shaped margin (urceolus) surrounding the stamens.

(7) *The ovary*—In *Heliocarpus* either borne upon a gynophore or sessile upon the gonophore, 2-celled, laterally compressed and ciliate about the margins; in *Triumfetta* always sessile upon the gonophore, 3- to 5-celled, not laterally compressed, and generally pubescent.

(8) *The style*—In *Heliocarpus* not more than three to four times the length of the ovary, usually much shorter, always bifid at the tip with the stigma lobes spreading; in *Triumfetta* usually longer than three to four times the length of the ovary, simple throughout, the stigma flattened or capitate.

Heliocarpus can be divided into two major groups of species based on the presence or absence of a gynophore in flower or fruit; further, the presence of appendages at the tips of the sepals is a character which is correlated in the majority of species (except in *H. mexicanus* and *H. nodiflorus*) with the absence of the gynophore.

---

[5]Critica Botanica (transl. by Hort and Green). Roy. Society, London. p. 79. 1938.

GEOGRAPHICAL DISTRIBUTION

The geographical range of *Heliocarpus* embraces nearly the whole of the tropical Americas. With the exception of the predominantly South American *H. popayanensis*, the species are indigenous entirely to Mexico and Central America. The presence of some plants of *H. popayanensis* in Hawaii apparently is due to recent introduction for reforestation in the foothills. Possibly in the same category is the presence of some plants of *H. Donnell-Smithii* in Martinique.

The species can be divided into five groups with respect to their geographical distributions:

(1) Northwestern Mexico—*H. attenuatus* and *H. Palmeri.*

(2) Southwestern Mexico—*H. terebinthinaceus, H. pallidus,* and *H. occidentalis.*

(3) South-central Mexico and Central America—*H. mexicanus, H. appendiculatus, H. Donnell-Smithii,* and *H. nodiflorus.*

(4) Southeastern Mexico—*H. americanus.*

(5) Southern Central America and South America—*H. popayanensis.*

The species of the sessile-fruited group are confined for the most part to the northern range of the distribution; while those of the stipitate-fruited group, where the fruits are borne upon bristly gynophores, are mostly in the middle and southern areas of distribution.

The northernmost limit of the genus is in subtropical Sonora and Chihuahua, Mexico, where the plants grow in canyon forests or oak flats; the southernmost limit is in central Argentina, where lower elevations along river banks are inhabited.

Except for shrubby plants *(H. occidentalis* and *H. pallidus)*, which sometimes grow on barren hill slopes, the majority of the species, consisting of small trees, grow only in moist places at higher elevations, usually at about 1000 m. or more, in rain- or cloud-forests, along roadways or river banks in sheltered places, or on edges of forests (usually on cut-over lands in second growth, where they sometimes form a pure stand).

ECONOMIC VALUE

In so far as is known from collectors' notes and from the published accounts of Standley[6] and Martinez[7], the economic importance of *Heliocarpus* is primarily in its bark, which produces a very strong and durable fibre. The bark of the young branches yields a fibre from which a strong but coarse rope is made. It is used also for weaving mats and baskets. The principal component of the Mexican fabric *belem* is the cordage extracted from the barks. Resistant paper formerly was made from the wood in Mexico; in Brazil it is still so used to some extent. The wood of the trees is soft and light and is used for floats and bottle-stoppers. Because of its lightness it has been used for rafts. The bark is used for *mecates* in Guate-

[6]Contr. U. S. Nat. Herb. 23:739. 1923.

[7]Plantas utiles de Mexico, p. 253. 1936.

mala, and a decoction is used in sickness of cattle, and sometimes is applied on sores. In Hawaii the trees have been planted on the foothills for reforestation.

VERNACULAR NAMES

H. americanus: *janote* (Vera Cruz).

H. appendiculatus: *burio, burio blanco,* and *burio colorado* (Costa Rica); *cajeton* (Guatemala); *balsa* and *pastano mula* (Nicaragua); *calagua* (El Salvador); *jonote, jonote blanco, jonote colorado* (Vera Cruz); *majao* (Honduras).

H. attenuatus: *samo baboso* (Sinaloa).

H. Donnell-Smithii: *holol* (Quintana Roo); *jolocin* (Tabasco); *jonote* (Vera Cruz); *majao* (Honduras); *moho,* "broad-leaved *moho*", and "mountain *moho*" (British Honduras).

H. mexicanus: *antigua, cajeto,* and *majagua* (Guatemala); *moho* (British Honduras).

H. nodiflorus: "broad-leaf *mohe*" (British Honduras); *cajeto* (Guatemala); *majao* (Honduras).

H. occidentalis: *pulmonilla, guasima,* and *panigua* (Chiapas and Jalisco).

H. pallidus: *guasima* and *tilia* (Guerrero, Jalisco, and Mexico).

H. Palmeri: *coche* (Sinaloa); *rama kowusamo,* and *palo chinu* (Sonora).

H. popayanensis: *balsa* (Colombia); *majagua* (Venezuela); *palo de balsa* (Peru); *sanpan* (Ecuador).

H. terebinthinaceus: *cuahualagua* or *quauhalagua* (Morelos and Puebla); *guasima, jolotzin, majorhua,* and *jonote* (Morelos, Oaxaca, and Guerrero).

ACKNOWLEDGMENTS

During the course of this study, materials from the following herbaria have been examined, for which I wish to acknowledge my indebtedness:

Jardin Principal de l'Etat, Bruxelles, Belgium.
Conservatoire Botanique, Genève, Switzerland.
Chicago Natural History Museum (Field), Chicago, Illinois.
Gray Herbarium of Harvard University, Cambridge, Massachusetts.
Royal Botanic Gardens, Kew, England.
Missouri Botanical Garden, St. Louis, Missouri.
New York Botanical Garden, New York, N. Y.
Royal Botanic Gardens of Trinidad and Tobago, Port-of-Spain, Trinidad, B.W.I.
University of California, Berkeley, California.
University of Michigan, Ann Arbor, Michigan.
United States National Herbarium, Washington, D. C.

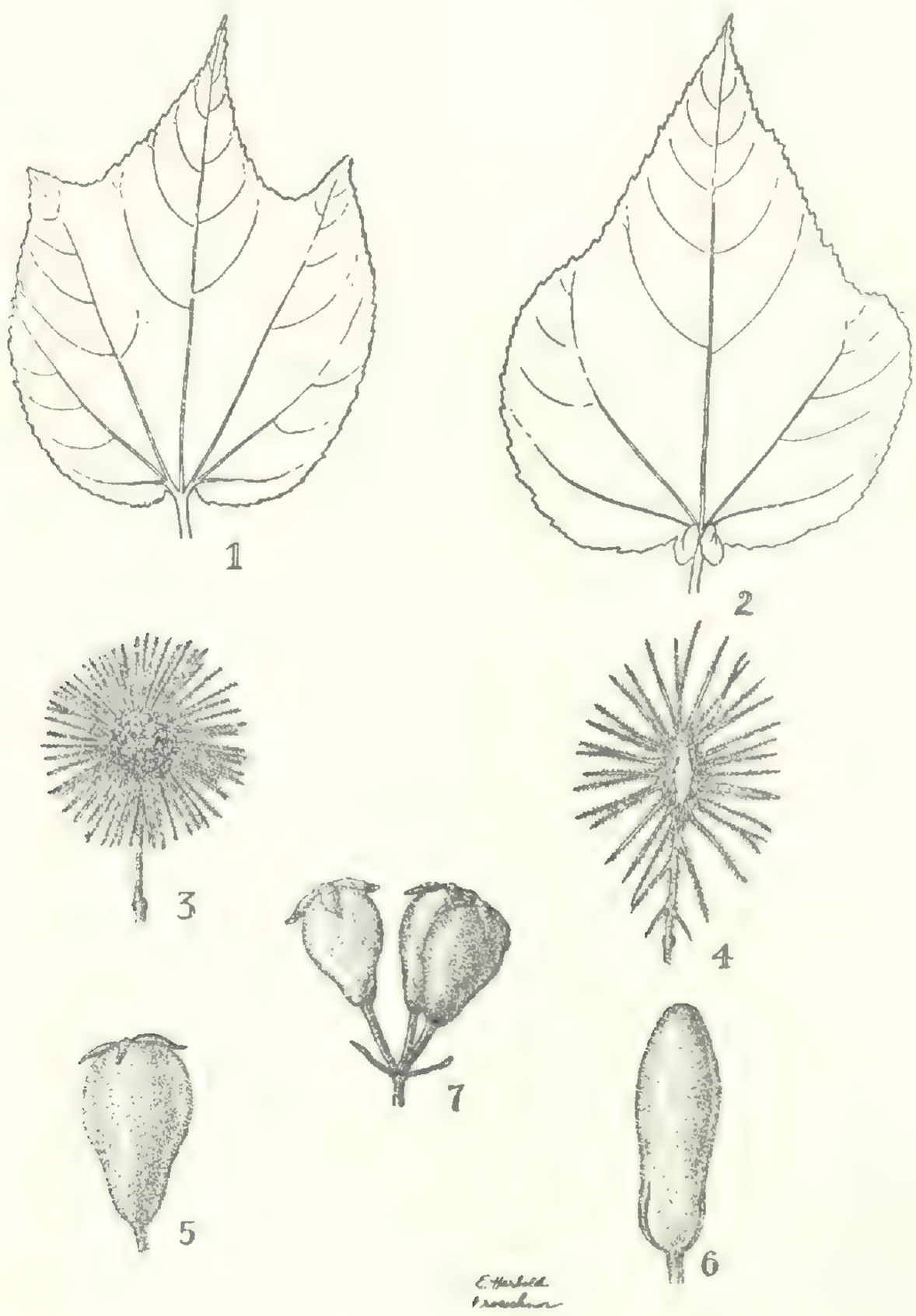
I am greatly indebted to the Missouri Botanical Garden and to its director, Dr. G. T. Moore, for the use of its library and herbarium facilities during the course of this study. Particular thanks are due to Dr. R. E. Woodson, Jr., for his advice, guidance, and constructive criticism.

TAXONOMY

HELIOCARPUS L. Sp. Pl. ed. 1. 448. 1753; Gen. Pl. ed.5. n. 606. 1754.

Adenodiscus Turcz. in Bull. Soc. Nat. Moscou 19[2]:504. 1846.

Woody trees or shrubs; older branches cream to brown, nearly glabrate, the younger branches usually stellate-pubescent, dark brown, fibrous, with many mucilage canals. Leaves alternate, petiolate, stipulate, the stipules usually large, early deciduous, very rarely persistent, the blade 3-lobed to undivided, venation palmate and either 5- to 7-costate or 3-costate at the base, irregularly serrated, the basal serrations usually glandular, slightly to densely stellate-pubescent, acute to



Illustrations of taxonomic criteria of the genus *Heliocarpus:* 1, leaf of *H. terebinthinaceus* showing the 3-costate venation at the base; 2, leaf of *H. appendiculatus* showing the 5-costate venation at the base and the 2 leafy auricles at the basal sinus; 3, sessile fruit of *H. occidentalis* showing the separate tufts of stellate hairs; 4, stipitate fruit of *H. Donnell-Smithii* borne on a bristly gynophore; 5, floral bud of *H. Palmeri* showing the relatively large, reflexed, trigonal appendages on the tips of the sepals; 6, floral bud of *H. appendiculatus* (note the absence of apical appendages); fig. 7, 3-radiate flowering peduncle (cymule) of *H. Palmeri* with a pair of bracteoles.

acuminate, the base rounded or cordate. Inflorescence gynodioecious or hermaphrodite, usually terminal (axillary in some species), large and spreading, consisting of numerous aggregate dichasia, the main axis branching sympodially and at each node bearing a cluster (cyme) of some 12–20 flowers, the terminal branches with 5–7 cymes, usually more or less secund, each cyme consisting of reduced sympodially branched axes terminating in 3- (rarely 2-) flowered cymules. Flowers either hermaphrodite or pistillate, regular, hypogynous, 4- to 5-merous; the sepals valvate, usually stellate-pubescent without, glabrate within, sometimes with small appendages at the tips; the petals 4–5 in hermaphrodite flowers, absent in the pistillate, free, valvate, 1- to 3-nerved, shorter than the sepals, usually ciliate at the base, sometimes slightly so at the apex; the stamens 12–40 in hermaphrodite flowers, staminodial or absent in the pistillates, borne cyclically on the enlarged gonophore, with 2-lobed, 4-celled, introrse, longitudinally dehiscent anthers; the ovary wholly superior, sessile upon the gonophore or with a manifest gynophore, ellipsoid to orbicular, laterally compressed, ciliate and with shorter pubescence on the faces, 2-celled, falsely 4-celled at the base, each cell with 2 anatropous ovules, the style filiform, bifid at the tip with the stigma lobes spreading and simple or slightly 3-lobed. Fruit dry, indehiscent, 2-celled, 2-seeded, laterally compressed, ellipsoid to orbicular, slightly rugose, sessile or stipitate upon the accrescent gynophore, ciliate with 2 rows of plumose bristles decurrent upon the gynophore when present, the faces pubescent to glabrate; the seed compressed-ovoid or -pyrifrom, with a median funicular groove, endosperm oily.

Standard species: *Heliocarpus americanus* L.

KEY TO THE SPECIES

A. Fruit sessile; ovary sessile on the gonophore.
  B. Leaves 3-lobed, veins 3-costate at the base; buds with or without appendages at the tips of the sepals.
    C. Leaves with dense, coarse pubescence on both surfaces, cordate, 3-lobed, about 14 cm. long and 12 cm. wide; buds sometimes with small appendages at the tips of the sepals; fruit spherical, tomentose; southwestern Mexico. . . . . 1. *H. terebinthinaceus*
    CC. Leaves with pale, smooth tomentum beneath, glabrate above, the base rounded to slightly cordate, 3-lobed to obscurely so, about 10 cm. long and 8 cm. wide; buds with conspicuous, erect appendages at the tips of the sepals; fruit ovoid, glabrate; southwestern Mexico ..... 2. *H. pallidus*
  BB. Leaves not lobed, veins 5- to 7-costate at the base; buds with conspicuous appendages at the tips of the sepals.
    C. Leaves cordate.
      D. Leaves nearly glabrate on both surfaces, about 14 cm. long and 10 cm. wide, acuminate; appendages on the sepals trigonal, large and reflexed; stamens about 40; style about 4 times longer than the ovary; fruit spherical, with a distinct groove in the body, slightly tomentose; northern Mexico..... 3. *H. Palmeri*
      DD. Leaves glabrescent above, tomentose beneath, small, about 8 cm. long and 5 cm. wide, caudate-acuminate; appendages on the sepals linear, erect; stamens 16–20; style about twice the length of the ovary; fruit ellipsoid, tomentose; northern Mexico ..... 4. *H. attenuatus*
    CC. Leaves rounded or cuneate at the base, glabrate or nearly so on both surfaces; appendages on the sepals short, erect; stamens about 40; style about twice the length of the ovary; fruit ovoid with short, separate tufts of stellate hairs; southwestern Mexico. ..... 5. *H. occidentalis*

AA. Fruit borne on a bristly gynophore; ovary borne on a gynophore upon the gonophore.
B. Inflorescences axillary, leafy; leaves not lobed, the base obtuse, glabrate above, slightly tomentose beneath; buds with conspicuous appendages at the tips of the sepals; stamens about 25–30; fruit ellipsoid. glabrous; southern central Mexico and Central America .....6. *H. mexicanus*
BB. Inflorescences generally terminal, not leafy.
C. Leaves with two conspicuous auricles at the basal sinus, usually not lobed, the base rounded or subcordate, glabrate above, tomentose beneath; buds without appendages at the tips of the sepals; stamens about 30; fruit suborbicular, tomentose; southern central Mexico and Central America.....7. *H. appendiculatus*
CC. Leaves without conspicuous auricles at the basal sinus.
D. Leaves not lobed, rounded at the base, not longer than 14 cm. or wider than 10 cm.
E. Leaves very densely tomentose beneath, glabrate above; stamens about 20; style very briefly bifid; fruit orbicular, tomentose; southeastern Mexico.....8. *H. americanus*
EE. Leaves glabrate on both surfaces; stamens about 12–16; style bifid about half its length; fruit ellipsoid, glabrate; southern central Mexico and Central America .....9. *H. Donnell-Smithii*
DD. Leaves generally 3-lobed, cordate at the base, about 17 cm. long and over 14 cm. wide.
E. Leaves glabrate above, the lower surface puberulent with short, stellate and long, simple hairs, especially on the veins; buds without appendages at the tips of the sepals; stamens about 12; style briefly bifid, each stigma with 3 acute lobes; fruit ovoid, slightly tomentose to nearly glabrate; southern Central America and South America.....10. *H. popayanensis*
EE. Leaves glabrate on both surfaces, veins not pubescent on the lower surface; buds sometimes with short appendages at the tips of the sepals; stamens about 24; style bifid about half its length, stigma-lobes simple, acute; fruit orbicular, slightly tomentose; southern Mexico and Central America.....11. *H. nodiflorus*

1. HELIOCARPUS TEREBINTHINACEUS (DC.) Hochr. in Ann. Conserv. et Jard. Bot. Genève 18:125. 1914.

Grewia terebinthinaceus DC. Cat. Hort. Monsp. 114. 1813. (T.: *Berlandier 1064*).
H. Nelsonii Rose, in Contr. U. S. Nat. Herb. 6:128. 1897. (T.: *Nelson 1485*).
H. reticulatus Rose, loc. cit. 128. 1897. (T.: *Pringle 1791*).
H. microcarpus Rose, loc. cit. 8:316. 1905. (T.: *Pringle 8719*).

Small trees or shrubs 4–5 m. high; older branches cream to brownish, glabrate, slightly longitudinally ridged, irregularly punctate with white lenticels; younger branches and inflorescence axes rough, scurfy, ferruginous-tomentose with stellate hairs. Leaves 3-lobed, acuminate, about 13–15 cm. long and 10–12 cm. wide, 3-costate, the mid-costa arising independently of the lateral costae, and each lateral costa consisting of 2 or 3 veins united at the basal sinus, base cordate, irregularly and bluntly serrated, both surfaces light green or pale brownish with thick, matted, stellate pubescence, the veins more pubescent with both stellate and long simple hairs; petioles slender, about 8 cm. long, covered with ferruginous tomentum. Inflorescences gynodioecious; the hermaphrodite usually axillary, rarely terminal, large and leafy, usually about 20 cm. long and 15 cm. wide, sometimes about 25 cm. long and 20 cm. wide, the cymes of about 15–18 flowers, rather compact in nodose clusters, the flowering peduncles 3-radiate, about 2 mm. long, the pedicels about 2 mm. long, the buds obovoid, constricted towards the base, sometimes with small erect appendages on the tips of the sepals, the sepals 4, spatulate, about 4–5

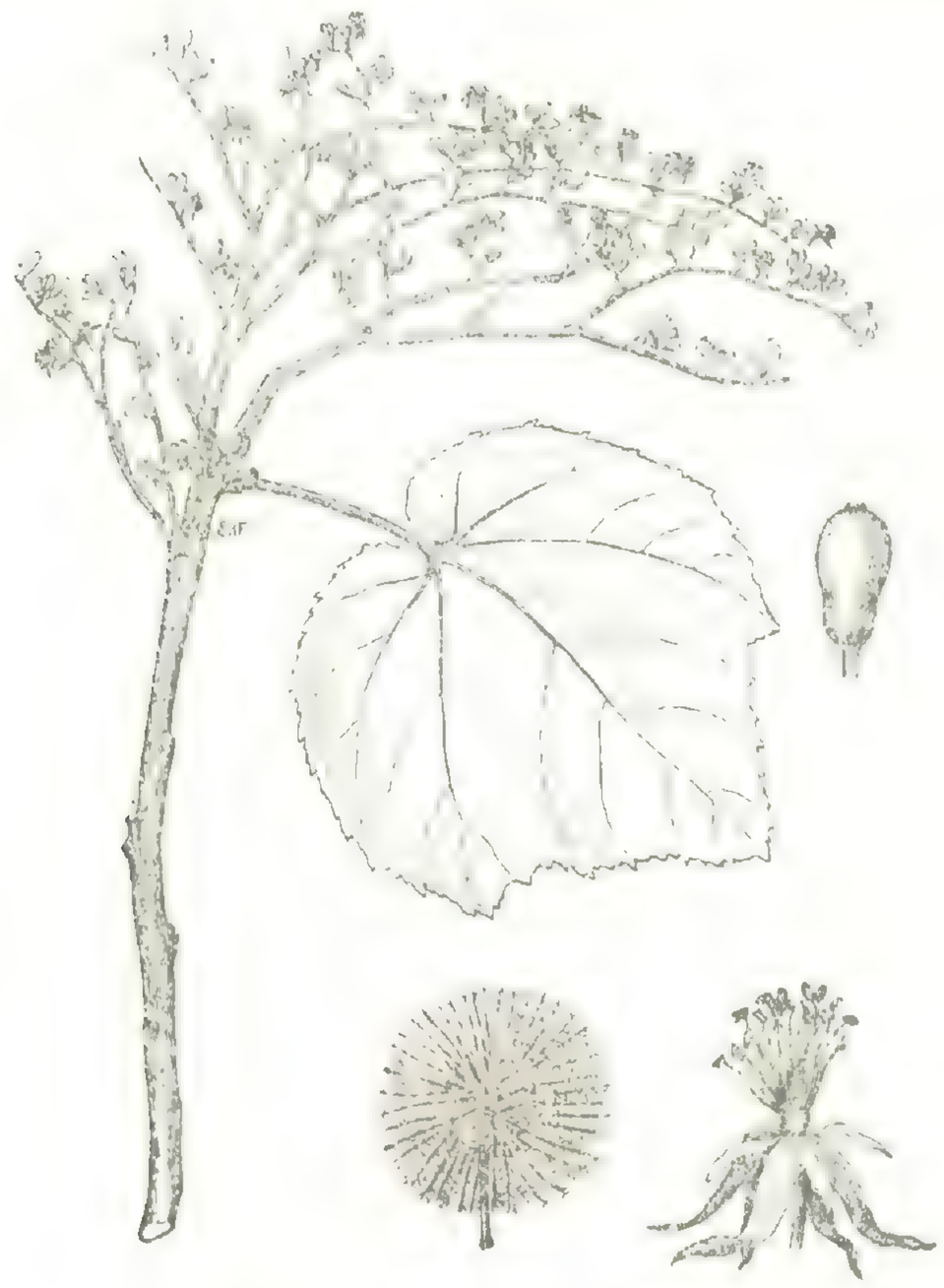
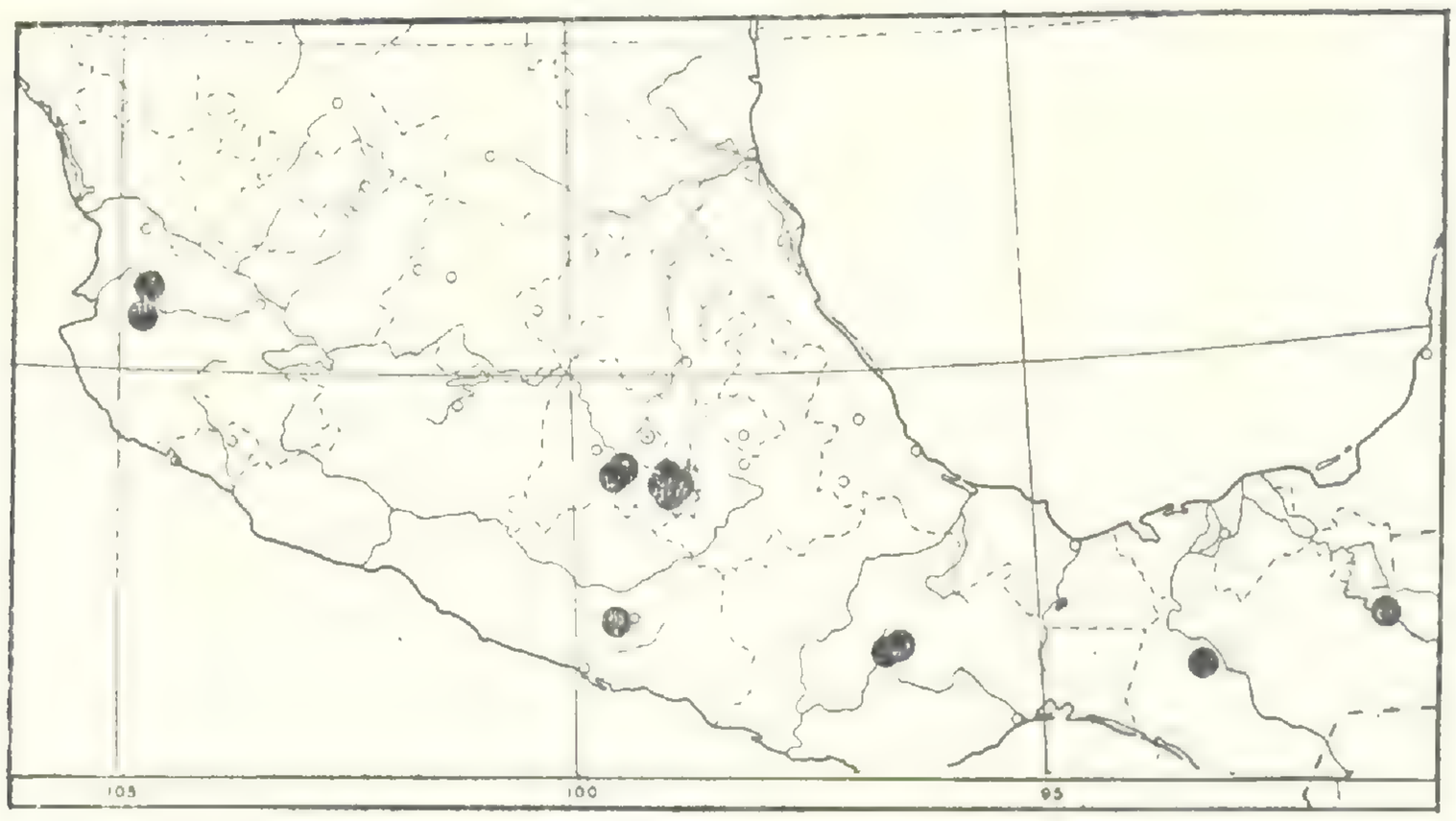


Fig. 1. *H. terebinthinaceus*

mm. long, densely stellate-tomentose without, glabrate within, the petals 4, linear, 1-nerved, about 3–4 mm. long, the ovary ellipsoid, about 1.5 mm. long, sessile, with a style about 3 mm. long, bifid about one quarter of its length and with stigma lobes acute, spreading; the pistillate much smaller than the hermaphrodite, about 10–15 cm. long and 8–10 cm. wide, the cymes of about 18 flowers, very much crowded in compact nodose clusters, the flowering peduncles 3-radiate, very short, less than 1 mm. long, the pedicels about 1–2 mm. long, the buds obovoid, not appendaged at the tips of the sepals, the sepals 4, linear, about 2 mm. long, densely stellate-tomentose without, glabrate within, the petals none, the staminodes about 10–12, the ovary ellipsoid, minute, sessile, with a style about twice the length of the ovary, briefly bifid at the tip, and with the stigma lobes acute. Fruit suborbicular, 4–5 mm. in diameter, rather densely tomentose, sessile, the fringe of two rows of plumose bristles about 5–7 mm. long; the seed ovoid, about 2 mm. long, with a very slight groove in the middle.

Distribution: On the highlands of central Mexico, especially on open hill slopes, altitude above 1000 m. Flowers throughout September and October, and fruits from late October to December.

MEXICO: CHIAPAS: Tuxtla Guttierez, *Juzepczuk 1461*. GUERRERO: above Chilpancingo, *Nelson 7046;* Sierra Madre, alt. 1250 m., *Langlassé 572*. JALISCO: road to San Domingo mine, alt. 5160 ft., Etzatlan, *Barnes & Land 285;* barranca, Guadalajara, alt. 4500 ft., *Pringle 9693;* Guadalajara, *Pringle 1791*. MEXICO: Tejupilco, Temascaltepec,



Map 1. Distribution of *H. terebinthinaceus*

Hinton 6736; Acatitlan, Temascaltepec, alt. 1130 m., *Hinton 5119.* MORELOS: Cuernavaca, alt. 5000 ft., *Pringle 8227;* lava field near Yantepec, alt. 4000 ft., *Pringle 9692;* vicinity of Cuernavaca, *Lemmon & Lemmon s. n.;* Cuernavaca, Atlacomulco, alt. 1300–1400 m., *Woronow 2333;* Cuernavaca, *Berlandier 1064;* Cuernavaca, *Bourgeau 1200;* about Cuernavaca, alt. 5000 ft., *Pringle 8719.* NAYARIT: El Trapiche, s. e. of Yxtian, alt. 1200 m., *Mexia 809.* OAXACA: Valley of Oaxaca, alt. 5100–5800 ft., *Nelson 1243;* Valley of Oaxaca, alt. 5500–7500 ft., *Nelson 1485;* on slopes east of Cincatlan, alt. 2500–4000 ft., *Nelson 1818;* Rio Blanco, San Juan del Estado, alt. 5000 ft., *L. C. Smith 797;* Monte Alban, alt. 6200 ft., *L. C. Smith 939;* Hacienda Guadalupe, alt. 1600 m., *Conzatti s. n.;* Tomellin Cañon, near city of Oaxaca, *Rose & Hough 4565.* DATA INCOMPLETE: Ahualulco ?, Barcena, *Urbina 639.*

This species is very distinct and can be recognized easily by its 3-lobed leaves with the characteristic venation, and also by its sessile fruits. Hochreutiner pointed out that *Berlandier 1064,* collected from Cuernavaca, which Rose cited for *H. Nelsoni,* is identical with the specimen which de Candolle, on the assumption of a 4-locular ovary, described as *Grewia terebinthinaceus.*

Rose differentiated his *H. Nelsoni* (type: *Nelson 1243* & *1485*), *H. reticulatus* (type: *Pringle 1791*) and *H. microcarpus* (type: *Pringle 8719*) primarily on the degree of pubescence on the fruits. This character is extremely variable. In matching the three types, it is noticeable that *H. microcarpus* has slightly smaller fruits and that the flowers have minute erect appendages. The size of the fruits varies slightly from plant to plant and sometimes on the same plant. Furthermore, the apical appendages on the sepals, when present, are extremely minute and not clearly seen. As they stood, it was difficult to tell the three species apart and there were many misdeterminations.

2. HELIOCARPUS PALLIDUS Rose, in Contr. U. S. Nat. Herb. 5:128. 1897. (T.: *E. Palmer 157*).

H. velutinus Rose, loc. cit. 8:317. 1905. (T.: *Pringle 8694*).

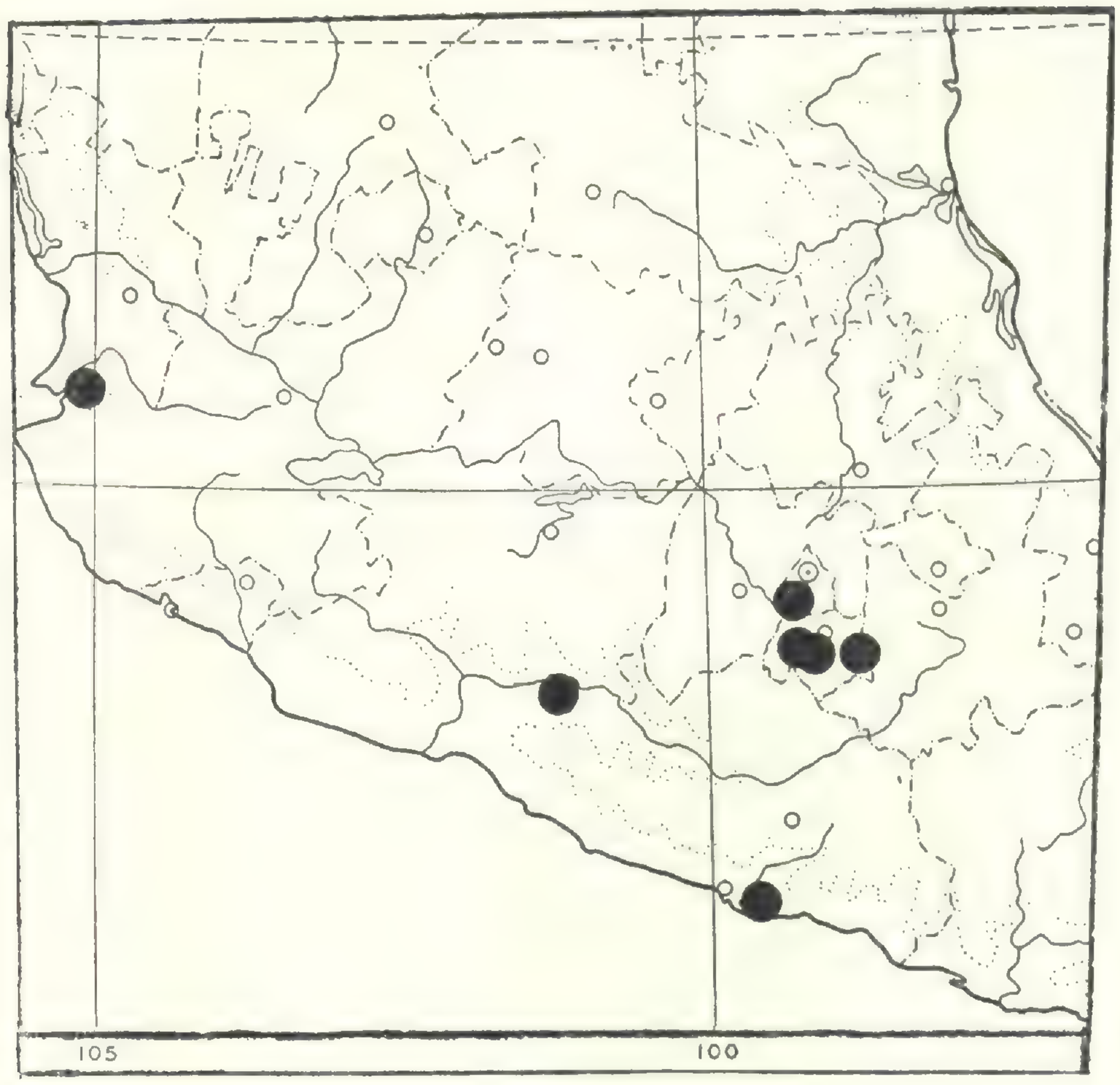
Fig. 2. *H. pallidus*

Small trees or shrubs about 2–4 m. high; older branches yellowish brown, glabrate, slightly rugose, punctate with few white lenticels; younger branches and inflorescence axes scurfy, slightly ferruginous-tomentose. Leaves small, younger ones generally not lobed or obscurely so, older ones 3-lobed, about 8–10 cm. long and 7–8 cm. broad, 3-costate, with the midcosta arising independently of the two lateral costae, and each lateral costa consisting of 2 or 3 veins united at the sinus, base usually cordate or subcordate, in younger leaves slightly rounded, acuminate, irregularly serrated, upper surface dark green, glabrate, lower surface whitish, densely stellate-tomentose with appressed hairs; petioles long and slender, 6–7 cm. long. Inflorescence hermaphrodite, usually axillary, large and spreading, leafy, about 14–20 cm. long and 12–20 cm. wide; the cymes of about 12–15 flowers borne loosely in nodose clusters, the flowering peduncles 3-radiate, about 2–3 cm. long, the pedicels about 4–5 mm. long, the buds obovoid, constricted at the base, with small linear, acute, erect appendages at the tips of the sepals, the sepals 4, linear, 4–6 mm. long, light green and slightly stellate-pubescent without, glabrate and yellowish within, the petals 4, linear, about 3–4 mm. long, the ovary ovoid, small, 0.5–1.0 mm. long, sessile, with a style about twice the length of the ovary, briefly bifid at the tip, and with the stigma lobes acute. Fruit ovoid, usually in compact clusters, very tomentose when immature, becoming glabrate at maturity, about 5 mm. long and 3 mm. wide, sessile, the fringe of two rows of plumose bristles about 4–5 mm. long; the seed obliquely ovoid, about 3 mm. long and 2 mm. wide, with a very deep groove in the middle.

Distribution: On the highlands of central and southwestern Mexico, especially on open hill slopes, altitude above 500 m. Flowers from October to November, and fruits in December and January. Usually leafless in January.

MEXICO: GUERRERO: Paso de las Vacas, *Nelson 6970;* Pungarabato, Coyuca, *Hinton 7243;* Acapulco and vicinity, *E. Palmer 157.* JALISCO: Puerto Vallarta, El Real, *Mexia 1100.* MEXICO: Chorrera, Temascaltepec, alt. 1350 m., *Hinton 5416;* Ocotepec, Temascaltepec, *Hinton 7036;* Tenayac, Temascaltepec, *Hinton 5109;* Chorrera, Temascaltepec, *Hinton 7236;* Ixtapan, Temascaltepec, *Hinton 7155.* MORELOS: near Yantepec, alt. 4500 ft., *Pringle 8694;* Cuernavaca, *Berlandier 071.* DATA INCOMPLETE: *Haenke 2468.*

The types of the two species *H. pallidus (E. Palmer 157)* and *H. velutinus (Pringle 8694)* have leaves which apparently look distinct, those of *H. pallidus* being small, obscurely 3-lobed, with rounded base, and of *H. velutinus* relatively



Map 2. Distribution of *H. pallidus*

small but definitely 3-lobed with subcordate base. It is apparent that the type of *H. pallidus* represents the immature and that of *H. velutinus* the mature state of the leaves. On the same branch (cf. *Hinton 5416* and *Mexia 1100*) the leaves at the base of the specimens may correspond to those of *H. velutinus* and those near the tip to *H. pallidus*.

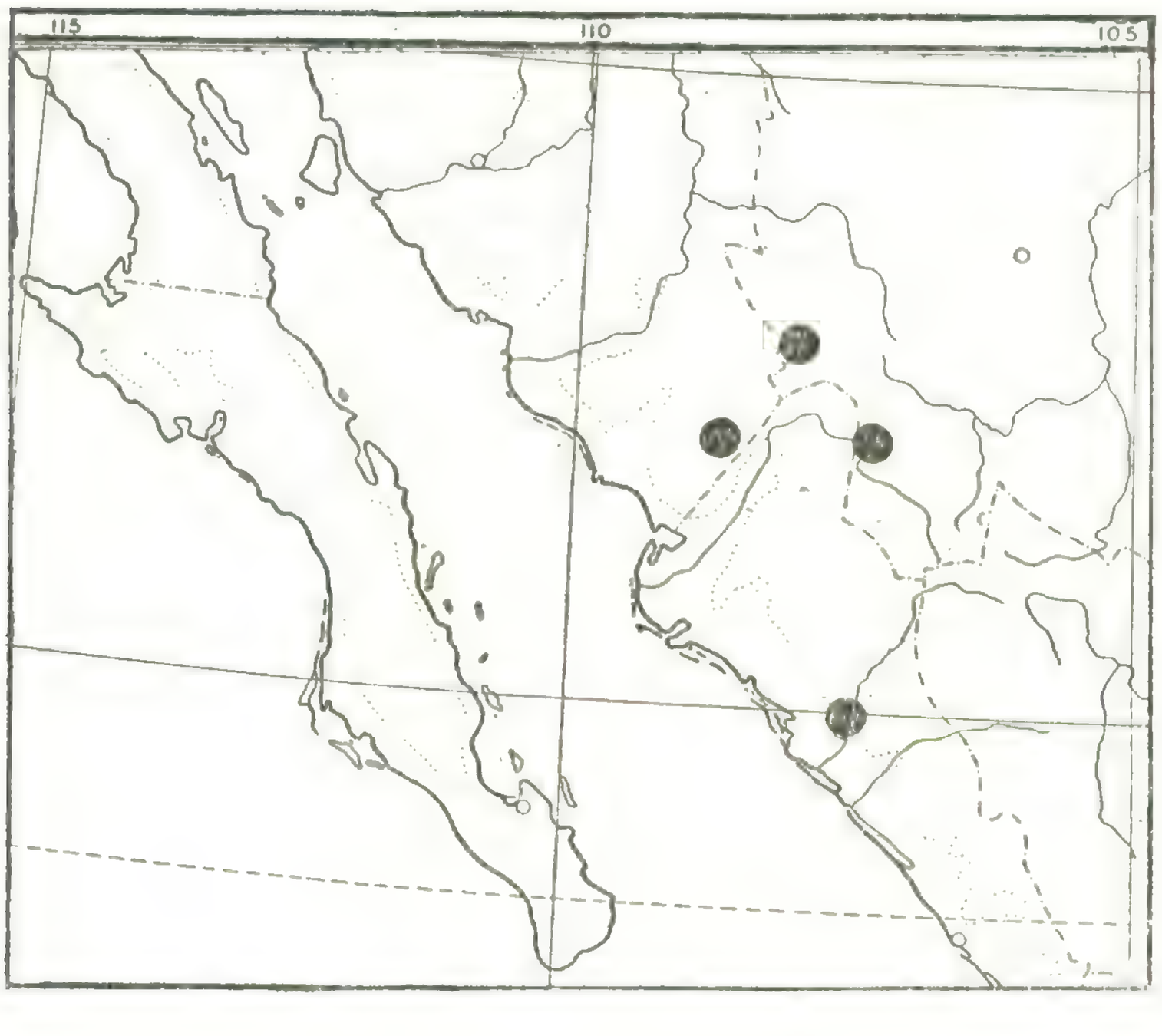
The fruits on the type of *H. velutinus* are slightly larger and more glabrate than those on the type of *H. pallidus*. There are many intermediates between these two extremes, in specimens that answer to the above descriptions. Presumably the fruit, which is slightly tomentose when young, becomes nearly glabrate at maturity.

3. HELIOCARPUS PALMERI S. Wats. in Proc. Amer. Acad. 21:420. 1886. (T.: *E. Palmer 191*).

H. polyandrus S. Wats. loc. cit. 1886. (T.: *E. Palmer 100*).
H. glaber Brandegee, in Zoe 5:207. 1804. (T.: *Brandegee s. n. in Herb. Calif.*).

Diffusely spreading shrubs about 2–3 m. high; older branches dark brown, glabrate with few short tufts of stellate hairs mostly around the white lenticels; younger branches and inflorescence axes covered lightly with short stellate tomen-

Fig. 3. *H. Palmeri*



Map 3. Distribution of *H. Palmeri*

tum. Leaves broadly ovate, 12–14 cm. long and 8–10 cm. wide, not lobed, 5-costate, narrowly acuminate, base cordate or subcordate, thin, unequally and bluntly serrated, basal serrations glandular, upper surface dark green, nearly glabrous to glabrate, rough, with few short suppressed, scattered tufts of stellate hairs, sometimes slightly scabrous on the veins, lower surface lighter green, slightly more pubescent than the upper, nearly glabrate, generally coarse, with short suppressed stellate hairs, veins scabrous, prominent; petioles slender, 5–7 cm. long, covered very lightly with short suppressed yellowish stellate pubescence. Inflorescence hermaphrodite, terminal, rarely axillary, slightly leafy, about 14 cm. long and 12 cm. wide, rarely larger, the cymes of about 12 flowers rather loose, the flowering peduncles 3-radiate, about 2 mm. long, the pedicels 3–4 mm. long, the buds obovoid, constricted towards the base, with conspicuous appendages at the tips of the sepals, the sepals 5, spatulate, 5–6 mm. long, 3-nerved, with large, about 2 mm. long, reflexed, trigonal appendages at the tips, light green with short suppressed tufts of stellate hairs without, glabrate, yellow to yellowish brown within, the petals 5, linear, slightly shorter than the sepals, about 4 mm. long, 1- to 3-nerved, yellowish brown, the stamens about 40, with filaments about 4–5 mm. long, the ovary orbicular, 1–2 mm. long, sessile, with a slender style about 4 times the length of the ovary, briefly bifid at the tip, and with small acute stigma lobes. Fruit orbicular, sessile, densely stellate-pubescent, 5 mm. in diameter, with a distinct groove in the middle of the fruit body, the fringe dense, of 2–3 rows of plumose bristles shorter than the diameter of the fruit body, about 3 mm. long; the seed plump, ovoid, very slightly grooved, about 2 mm. long.

Distribution: On shady canyon slopes or oak flats in northwestern Mexico, altitude about 500 m. Flowers in September–October and fruits in late October–December.

MEXICO: CHIHUAHUA: Hacienda San Miguel, near Batopilas, *E. Palmer 97, 100, 191;* Guasaremos, Río Mayo, *Gentry 2440, 2909;* La Mesa, *Gentry 6607;* Almaden, *Le Sueur 1404.* SINALOA: Cerro Colorado, alt. 2000 ft., *Gentry 5069;* vicinity of Culican, *Brandegee s. n.* (type of *H. glaber*). SONORA: Canyon Sapopa, Río Mayo, *Gentry 1644, 1709.*

A very distinct species with nearly glabrous leaves and sessile fruits characteristically grooved in the middle and with flowers bearing relatively large trigonal apical appendages on the sepals.

The leaves in the type of *H. Palmeri (E. Palmer 191)* are slightly more pubescent than those of *H. polyandrus (E. Palmer 100)*, but in both they are nearly glabrous and the variation is only one of slight degree. S. Watson mentioned that in *H. Palmeri* the number of stamens is about 20, but I have not been able to find any specimen that answers to the description of *H. Palmeri* with 20 stamens, either in the specimens cited by S. Watson or in others.

4. HELIOCARPUS ATTENUATUS S. Wats. in Proc. Amer. Acad. 21:420. 1886. (T.: *E. Palmer 99*).

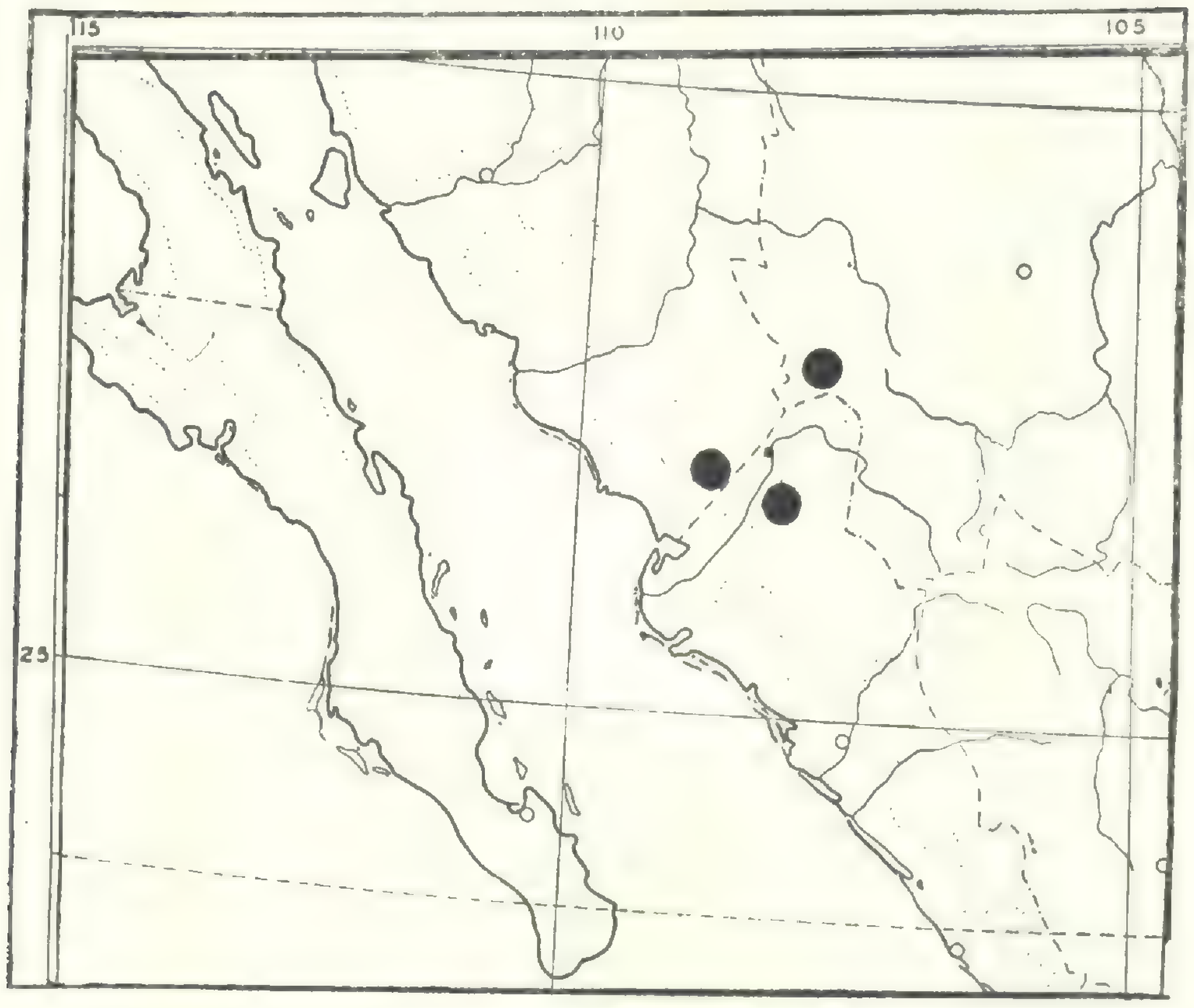
H. viridis E. E. Wats. in Bull. Torr. Bot. Club 50:120. 1923. (T.: *Rose, Standley & Russell 12828*).

Small shrubs about 2–3 m. high; older branches dark brown, rather slender, slightly pubescent, smooth, irregularly punctate with few white lenticels; younger branches and inflorescence axes softly tomentose with relatively long, light yellowish brown, stellate hairs, smooth. Leaves ovate to very obscurely 3-lobed, 5-costate at the base and gradually tapering to the caudate-acuminate tip, base cordate or subcordate, irregularly and bluntly serrated, upper surface slightly pubescent, coarse, with many suppressed stellate hairs, scabrous on the veins, lower surface densely stellate-pubescent especially on the veins. Inflorescence hermaphrodite, usually axillary, small, leafy, about 8 cm. long and 10 cm. wide, rarely larger, the cymes of about 16–18 flowers borne loosely in nodose clusters, the flowering peduncles mostly 3-radiate, rarely 2-radiate, about 5–6 cm. long, usually subtended by two short bracteoles, the pedicels 2–3 mm. long, the buds obovoid, very slightly constricted towards the base, with short appendages on the tips of the sepals, the sepals 3 or 4, linear, 4–5 mm. long, 1- to 3-nerved, the short, erect appendages on the tips 1 mm. long, light green with fine tomentum without, glabrate, yellowish brown within, the petals 3 or 4, linear, shorter than the sepals, 2–3 mm. long, the stamens about 16–20, with the filaments as long as the petals, the ovary ovoid, 1.0–1.5 mm. long, sessile, with a style about twice the length of the ovary, bifid about one quarter of its length and with the stigma lobes acute, spreading. Fruit ovoid, sessile, densely tomentose, 3 mm. long and 2 mm. wide, the fringe of two rows of slender plumose bristles, 6–7 mm. long; the seed ovoid, 1–2 mm. long.

Fig. 4. *H. attenuatus*

Distribution: Confined entirely to northwestern Mexico, apparently rare, usually growing at altitudes of about 300–500 m. Flowers from August to September and fruits from October to December.

MEXICO: CHIHUAHUA: southwestern Chihuahua, *E. Palmer 99;* Río Benito, *Le Sueur 661, 1158.* SINALOA: Choix, Tasfera, alt. 420 m., *Gonzalez 860.* SONORA: Alamos, *E. Palmer 647, 733;* Sierra de Alamos, *Rose, Standley & Russell 12828.*



Map 4. Distribution of *H. attenuatus*

This is a very distinct species, with the caudate-acuminate leaves the smallest known for the genus. It does not resemble any other species in its vegetative characters. The leaves of the type of *H. viridis (Rose, Standley & Russell 12828)* are small but not caudate-acuminate. The type is from a relatively young plant and rather poorly preserved. I have not been able to find any other specimen which matches the type, and I am doubtful about the type itself. Except for its small wrinkled leaves, there is nothing which would prevent its identification with *H. attenuatus* (type: *E. Palmer 99*).

5. HELIOCARPUS OCCIDENTALIS Rose, in Contr. U. S. Nat. Herb. 5:127. 1897. (T.: *Palmer 440*).

H. laevis Rose, loc. cit. 8:317. 1905. (T.: *Rose 2860*).

Small trees or shrubs about 5–6 m. high; older branches generally glabrate, cream to brownish, slightly rugose, irregularly punctate with white lenticels; younger branches and inflorescence axes covered with rather dense tomentum of short yellowish stellate hairs. Leaves broadly ovate, sometimes rather obscurely 3-lobed, 10–13 cm. long and 8–11 cm. wide, 5- to 7-costate at the base, narrowly acuminate, base rounded or cuneate, rarely subcordate, somewhat regularly and doubly serrated, upper surface generally dark green, glabrate, coarse, with suppressed stellate hairs, veins and veinlets more pubescent with short tufts of yellowish stellate hairs, lower surface slightly more pubescent than the upper, becoming

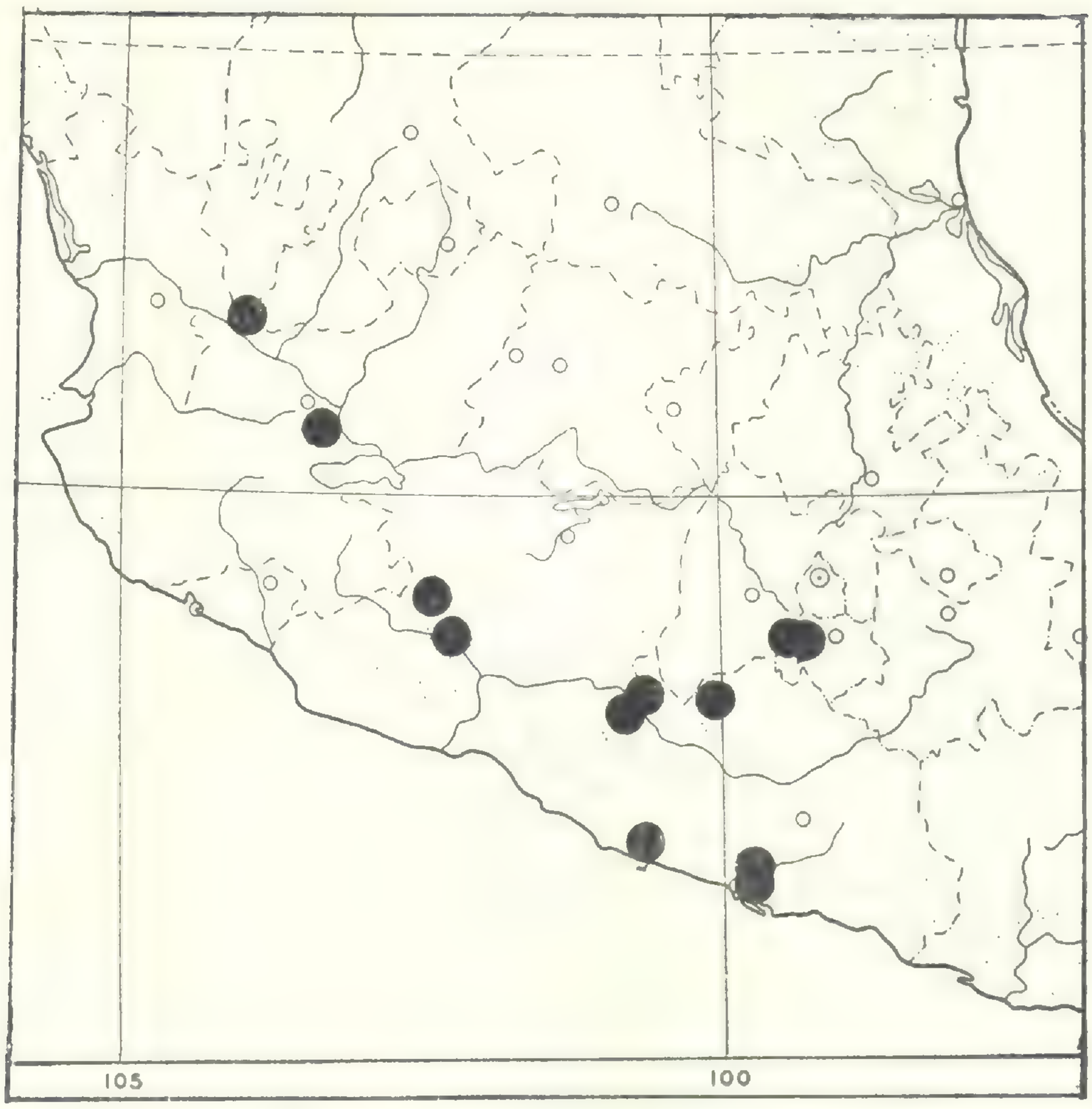
Fig. 5. *H. occidentalis*

nearly glabrate when mature, yellowish green, the veins and veinlets covered with dense tufts of yellow stellate hairs; petiole about 6 cm. long, slender, covered lightly with yellow stellate hairs. Inflorescences hermaphrodite, usually axillary, rarely terminal, rather leafy, about 14 cm. long and 10 cm. wide, sometimes much smaller, the cymes of about 12 flowers, rather loose in nodose clusters, the flowering peduncles 3-radiate, about 2 mm. long, subtended by two small bracteoles, the pedicels 2–3 mm. long, the buds obovoid, slightly constricted towards the base, with conspicuous appendages at the tips of the sepals, the sepals 5, rarely 4, linear-spatulate, 4–5 mm. long, 3- to 5-nerved, with small, about 1 mm. long, erect, linear appendages at the tips, light green with short stellate hairs without, glabrate, cream or light brown within, the petals 5, rarely 4, linear, nearly as long as the sepals, 1- to 3-nerved, the stamens about 40, with the filaments about 4–5 mm. long, the ovary ovoid, 1.0–1.5 mm. long, sessile, with a short style about twice the length of the ovary, briefly bifid at the tips and with small acute stigma lobes. Fruit orbicular, sessile, punctate with short separate tufts of stellate hairs, about 3 mm. in diameter, the fringe of relatively stout plumose bristles about 8–9 mm. long; the seed ovoid, about 2 mm. long.

Distribution: Plants of central Mexico, growing on hill slopes and chaparrals, between 500 and 1000 m. Flowering in September and October and fruiting from October to December.

MEXICO: CHIAPAS: Manzanillo, *E. Palmer 986.* GUERRERO: Acapulco, *E. Palmer 440;* La Providencia, Acapulco, *Hancock 12;* Iguala Canyon, alt. 2500 ft., *Pringle 10069;* Arecelia-Fraguas, Coyuca, *Hinton 6605;* Coyuca, *Hinton 6901, 6906;* Pungarabato, Coyuca, *Hinton 6876;* Atoyac, Galeana, *Hinton 10901.* JALISCO: Bolanos, *Rose 2860a, 2860b;* Guadalajara, *Rose & Painter 7389.* MEXICO: Limones, Temascaltepec, alt. 910 m., *Hinton 6724;* Paso del Río, *Emrick 192.* MICHOACAN: Apatzingan, alt. 2000 ft., *Leavenworth & Hoogstraal 1731;* between Acahuato and Apatzingan, *Leavenworth & Hoogstraal 1525;* El Ocote, *Langlassé 623.*

The fruits of this species are very characteristic, being nearly orbicular, with short separate tufts of stellate hairs. The small erect sepal appendages and the glabrate leaves make this species an easy one to identify. *H. laevis* (type: *Rose 2860*) which has been identified with many other species actually is conspecific with this.



Map 5. Distribution of *H. occidentalis*

6. HELIOCARPUS MEXICANUS (Turcz.) Sprague, in Kew Bull. 272. 1921. (T.: *Galeotti 4154*).

Adenodiscus mexicanus Turcz. in Bull. Soc. Nat. Mosc. 19^2:504. 1846.
Triumfetta mexicana Turcz. in loc. cit. 31^1:230. 1858.
H. glanduliferus Robinson, in Contr. U. S. Nat. Herb. 5:127. 1897. (T.: *Heyde 281*).
H. glabrescens Hochr. in Ann. Conserv. et Jard. Bot. Genève 18:122. 1914. (T.: *Galeotti 4154*).
H. costaricensis Sprague, in Kew Bull. 349. 1923. (T.: *Pittier 13022*).
H. belizensis Lundell, in Phytologia 2:2. 1941. (T.: *Gentle 2273*).
H. yucatenensis Millsp. in herb.

Small trees or shrubs 5–6 m. high; older branches dark brown, glabrate, slightly rugose, punctate irregularly with minute white lenticels; younger branches and inflorescence axes very lightly scurfy-pubescent, with small clusters of simple and stellate hairs, nearly glabrate. Leaves broadly ovate to ovate-lanceolate, the more mature ones broadly ovate, the younger ones around the inflorescence usually ovate-lanceolate, 5-costate at the base, not lobed, 12–14 cm. long and 6–10 cm. wide, acute to acuminate, base rounded or slightly obtuse, irregularly and bluntly serrated, the basal serrations glandular, upper surface dark green, glabrate with few suppressed stellate hairs, lower surface more pubescent with fine, weak, crisped, stellate

Fig. 6. *H. mexicanus*

Map 6. Distribution of *H. mexicanus*

hairs, becoming nearly glabrate at maturity. Inflorescences gynodioecious, axillary, large and very leafy; the hermaphrodite large and spreading, very leafy, about 20 cm. long and 15 cm. wide, the cymes of about 20 flowers, rather loose, the flowering peduncle mostly 3-radiate, about 2–3 mm. long, usually subtended by a pair of small blunt bracteoles, the pedicel about 6–8 mm. long, the buds obovoid, slightly constricted in the middle towards the base, rusty brown, with small appendages at the tips of the sepals, the sepals usually 5, rarely 4, spatulate, about 5–6 mm. long, 1–2 mm. wide, rusty brown and glabrate without, lighter brown and glabrate within, with linear, about 1.5 mm. long, erect appendages on the tips, the petals 5, rarely 4, linear, 1-nerved, 3–4 mm. long, the stamens 24–30, with the filaments as long as the petals, the ovary ellipsoid, 1–2 mm. long, borne on a very short gynophore, with a style about 3 times the length of the ovary, briefly bifid, and with acute, slightly spreading stigma lobes; the pistillate nearly as large as the hermaphrodite, the cymes of about 20 flowers, greatly condensed and crowded in nodose clusters, the flowering peduncles 3-radiate, short, less than 1 mm. long, the pedicels about 1 mm. long, the buds about 2–3 mm. long, appendaged at the tips of the sepals, the sepals 5, linear, about 3 mm. long, appendaged at the tips, rusty brown and glabrate without and within, the petals none, the staminodes about 20–30, the ovary ovoid, less than 1 mm. long, borne on a very short gynophore, with a short style, briefly bifid and with acute stigma lobes. The fruit ellipsoid, glabrate, surface red-glandular, about 6–8 mm. long and 3 mm. wide, with few ridges, borne on a bristly gynophore 2–8 mm. long, the fringe usually of one row of plumose bristles 6–8 mm. long; the seed pyriform, blunt-pointed, about 3–4 mm. long.

Distribution: Plants of southeastern Mexico and northern Central America, growing along roadways, river banks, or on hill slopes; in thickets of bushy slopes or on hill tops in open places. Flowers from September to October and sometimes as late as December, and fruits from November to February.

MEXICO: CAMPECHE: Tuxpena, *Lundell 959, 1192.* OAXACA: locality not mentioned, *Ghiesbreght 51.* VERA CRUZ: Zacuapan, *Linden 898;* Cordillera, *Galeotti 4154;* Zacuapan and vicinity, *Purpus 2227;* Mirador, *Liebmann 523;* Mirador, *Linden 858;* rocky barranca near Gaucho, Viejo, *Purpus 15704a.* YUCATAN: Pocoboch, Chac tolol, *Gaumer 1315;* San Anselmo, *Gaumer 1234;* Calotmul, *Gaumer 2302;* Chichankanab, *Gaumer 2275;* Xnocao, *Gaumer 23488, 24177.*

BRITISH HONDURAS: El Cayo District, Vaca, *Gentle 2273;* Jacinto Hills, alt. 600 ft., *Schipp S-589.*

GUATEMALA: ALTA VERAPAZ: southwest of Lanquin, alt. 600–1000 m., *Steyermark 44076.* CHIMALTENANGO: along Río Guacalate, southwest of Chimaltenango, alt. about 1700 m., *Standley 80064, 81067;* Chimaltenango, *Johnston 1106, 1332.* CHIQUIMULA: Volcán Ipala, near Amatillo, alt. 900–1510 m., *Steyermark 30377.* GUATEMALA: exact locality lacking, *Aguilar 81;* alt. 1485 m., *Morales 1.122.* JUTIAPA: Volcán Suchitan, northwest of Asuncion Mita, alt. 600–2050 m., *Steyermark 31912.* SACATEPEQUEZ: near Pastores, alt. 1560–1650 m., *Standley 59888;* near Antigua, alt. 1500–1600 m., *Standley 64273.* SANTA ROSA: above Cerro Redondo, *Steyermark 52218;* near Cuilapilla, alt. about 900 m., *Standley 78068;* Chupadero, alt. 5000 pp., *Heyde & Lux 3956.* DATA INCOMPLETE: *Heyde 381.*

HONDURAS: EL PARAISO: Guinope, alt. 1430 m., *Rodriguez 1679.*

El Salvador: vicinity of San Salvador, *Renson 61*; vicinity of San Salvador, alt. 650–850 m., *Standley 19660*.

Costa Rica: san josé: Río Torres, alt. 1100 m., *Tonduz 7451*; bords de Río Torres près San Francisco de Guadalupe, alt. 1100 m., *Tonduz 8453*.

This species has been described by most authors as having sessile fruits. Actually the fruits are borne on a gynophore the length of which varies from 2 to 8 mm. Many species have been named because of the extreme variability of the length of the gynophore. The correlation of the flowering with the fruiting specimens has been greatly confused.

H. mexicanus (type: *Galeotti 4154*) can be recognized easily by its brown glabrate fruits borne either on a very short or on a slightly longer gynophore. In flower, this is one of the easiest species to identify because of the large erect appendages on the tips of the sepals and the nearly glabrate ovate-lanceolate leaves, as well as by the leafy axillary inflorescence.

This species actually is a link between the sessile-fruited and the stipitate groups. It has the characteristics of both the groups.

7. Heliocarpus appendiculatus Turcz. in Bull. Soc. Nat. Moscou 31^1:226. 1858. (T.: *Linden 2065*).

H. chontalensis Sprague, in Kew Bull. 350. 1923. (T.: *Lévy 483*).

Trees 12–14 m. high; older branches dark brown, scurfy, ferruginous-tomentose with both simple and stellate hairs, rarely glabrate, ridged, punctate irregularly with small, white lenticels; younger branches and inflorescence axes covered with thick, scurfy, ferruginous tomentum. Leaves broadly ovate, sometimes obscurely 3-lobed, 14–16 cm. long and 12–14 cm. wide, 5- to 7-costate at the base, acuminate, base subcordate or rounded, with two conspicuous leafy auricles at the basal sinus, each about 5–7 mm. wide and 4–5 mm. long, unequally and bluntly serrated, the basal serrations glandular, upper surface dark green, glabrate, with few suppressed, compact tufts of stellate hairs, lower surface whitish, with dense stellate tomentum, petioles relatively stout, about 6–8 cm. long, covered with dense scurfy, ferruginous tomentum. Inflorescences hermaphrodite, usually terminal, rarely axillary, slightly leafy, about 15 cm. long and 12–14 cm. wide, the cymes of about 16–18 flowers, rather loose, the flowering peduncles 3-radiate, about 2–3 mm. long, the pedicels 3–4 mm. long, the buds obovoid, slightly constricted in the middle, rather large for the genus, about 6 mm. long, not appendaged at the tips of the sepals, the sepals 4, linear, 6–7 mm. long, light green with short separate tufts of stellate hairs without, glabrate, yellow-brown within, the petals 4, spatulate, 3-nerved, 3–4 mm. long, the stamens about 30, with filaments about 4–5 mm. long, the ovary ellipsoid, 1–2 mm. long, borne upon a gynophore about the length of the ovary itself, with a style about twice the length of the ovary, bifid about half its length and with small, acute, spreading stigma lobes. The fruit suborbicular, about 5 mm. long and 3–4 mm. wide, densely tomentose, borne upon a gynophore about 5–8 mm. long, with 2–3 pairs of plumose bristles, the fringe of 1 or 2 rows of plumose bristles about 6–8 mm. long; the seed pyriform with a shallow groove, slightly stellate-pubescent, about 2–3 mm. long.

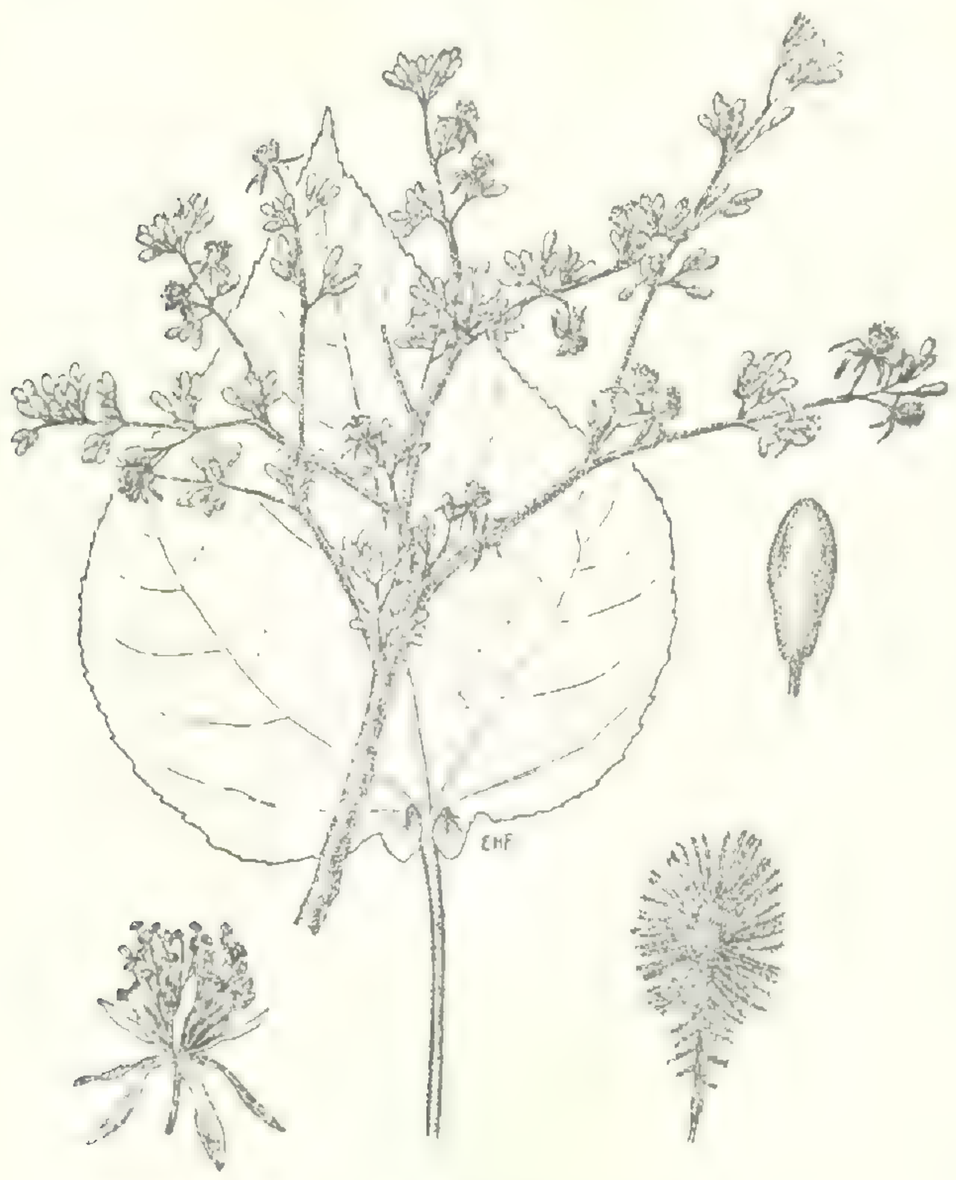


Fig. 7. *H. appendiculatus*

Map 7. Distribution of *H. appendiculatus*

Distribution: Plants of central Mexico and Central America: a species of relatively wide distribution, usually growing along river banks or roadways in secondary growth subjected to seasonal floods; at times forming a pure stand in moist places, usually in heavy red clay loam, at various altitudes but most abundant above 1000 m. Flowers from December to about the middle of March and fruits persistent up to about the middle of June.

MEXICO: SAN LUIS POTOSI: near Tancanhuitz, *Nelson 4383*. TABASCO: locality lacking, alt. 300 m., *Linden 1609;* Teapas, *Linden 2065*. VERA CRUZ: Fortuno, Coatzacoalcos River, alt. 30–50 m., *L. Williams 8273, 8288, 8280, 8400, 8526, 8527;* Río Seco prope Cordoba, *Woronow 2963;* Mirador, *Linden 460;* near Jalapa, *Rose & Hough 4314*.

GUATEMALA: ALTA VERAPAZ: Pansamala, alt. 3800 pp., *J. D. Smith 1723;* 2½ miles west of Cubilquitz, alt. 250–300 m., *Steyermark 44342;* trail from Senahu to Actala, *Maxon & Hay 3305, 3306, 3322;* Cubilquitz, alt. 350 m., *Tuerckheim 7828*. HUEHUETENANGO: between Maxbal and Xoxlac, Sierra de los Cuchumatanes, alt. 1500–1600 m., *Steyermark 48087;* Cerro Chiblac, between Finca San Rafael and Ixcan, Sierra de los Cuchumatanes, alt. 1200–2000 m., *Steyermark 49160*.

HONDURAS: ATLANTIDA: Lancetilla Valley, near Tela, alt. 20–600 m., *Standley 54096*.

NICARAGUA: SEGOVIA: region of Braggman's Bluff, *Englesing 136, 140;* Chontales, alt. 600 m., *Lévy 483;* Chontales, *Tate 31 (384)*.

COSTA RICA: CARTAGO: Rubber Plant Investigation Station, Turrialba, *Aguilar 07100*. GUANACASTE: upper slopes of Cerro San José de Libano, alt. 500–900 m., *Dodge, Hanckel & Thomas 6379*. SAN JOSÉ: vicinity of El General, alt. 700 m., *Skutch 3922;* vicinity of El General, alt. 670 m., *Skutch 4226*. DATA INCOMPLETE: *Rowlee & Rowlee 212;* Tibarcia, alt. 980 m., *Solis R. 534;* Santiago, *Brenez 655*.

An extremely easy species to identify due to the presence of two conspicuous auricles at the basal sinus of the relatively large leaf. The fruits are suborbicular and tomentose.

8. HELIOCARPUS AMERICANUS L. Sp. Pl. ed. 1, 448. 1753. (T. *in Br. Mus.*).[8, 9]

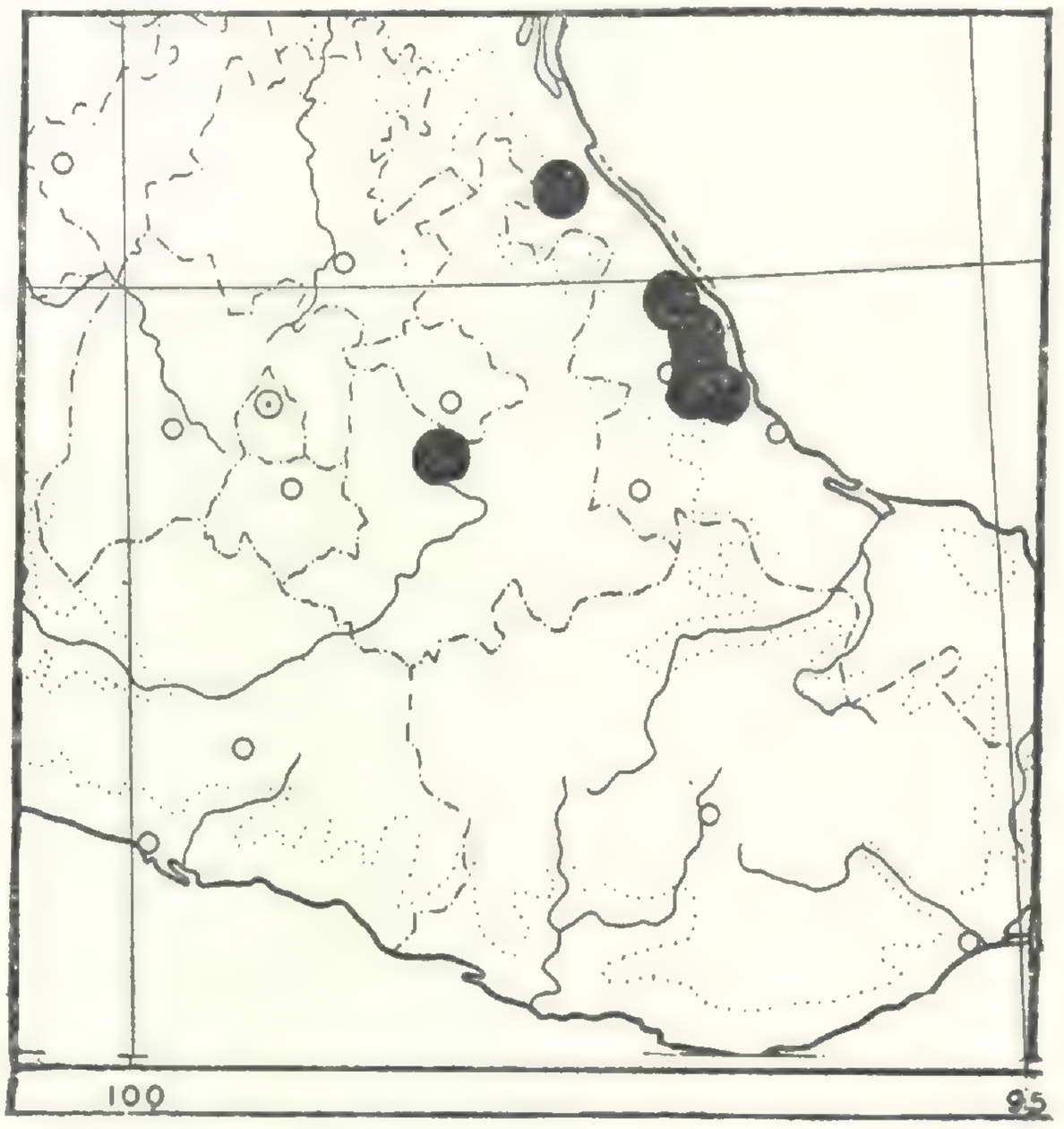
H. tomentosus Turcz. in Bull. Soc. Nat. Moscou 31:255. 1858. (T.: *Linden 857*).
H. americanus var. *typica* K. Schum. in Martius, Fl. Bras. 12[3]:141. 1886.

Small trees 3–5 m. high; older branches light brown, glabrate, smooth, irregularly punctate with many small white lenticels; younger branches and inflorescence axes lightly tomentose with both stellate and simple hairs. Leaves ovate, not lobed, 10-12 cm. long and 6–8 cm. wide, 5-costate at the base, acuminate, base rounded or obtuse, never cordate, irregularly and bluntly serrated, upper surface dark green, glabrate with few highly suppressed stellate hairs, lower surface whitish, very densely tomentose with both long stellate and simple hairs; petioles relatively stout, about 4 cm. long, very densely tomentose. Inflorescences hermaphrodite, terminal, about 15 cm. long and 12 cm. wide, sometimes very slightly leafy, the cymes of about 18–20 flowers, densely crowded in nodose clusters, the flowering peduncles 3-radiate, short, about 1 mm. long, the pedicels about 1–2 mm. long, the buds obovoid, slightly constricted towards the base, without appendages at the tips of the sepals, the sepals 4, spatulate, 4–5 mm. long, light green and densely tomentose without, glabrate, yellow to yellow-brown within, the petals 4, linear, 1-nerved,

[8] Jour. Bot. 36:131. 1898.
[9] Bot. Gaz. 61:256. 1923.

about 2–3 mm. long, the edges slightly ciliate, the stamens about 20, with the filaments about 3 mm. long, the ovary ovoid, about 1 mm. long, borne on a short gynophore, with a style about 2–3 times the length of the ovary, bifid about one quarter of its length and with acute, spreading stigma lobes. Fruit ovoid, densely tomentose, becoming slightly less so with age, about 3–4 mm. long and 2–3 mm. wide, borne on a long bristly gynophore about 5–8 mm. long, with 2–3 pairs of plumose bristles, the fringe of two rows of plumose bristles about 4–6 mm. long; the seed ovoid, about 1.5 mm. long and 1.0 mm. wide, with a distinct groove in the middle, slightly stellate-pubescent.

Fig. 8. *H. americanus*



Map 8. Distribution of *H. americanus*

Distribution: Plants of central and southeastern Mexico, growing at altitudes between 400–1200 m. Flowers in January and February and the fruits are persistent up to the middle of May.

MEXICO: OAXACA: locality not mentioned, *Galeotti 4162, 4162b.* PUEBLA: Huauchinango, convalles torrentis, alt. 1100 m., *Fröderström & Hulten 860.* VERA CRUZ: Zacuapan and vicinity, *Purpus 2226, 2387;* Zacuapan, *Purpus 8275;* Mirador, *Liebmann 475;* Orizaba, *Botteri 340, 341, 882, 888, 922;* Vallee de Cordova, *Bourgeau 1819, 1974;* Mirador, alt. 400 m., *Linden 857;* Cordova, *J. G. Smith 284;* near Jalapa, *Rose & Hough 4304;* Estacion El Fortin, Orizaba, *Conzatti 1694;* near Orizaba, alt. 4000 ft., *Pringle 6106;* Sanborn, *Orcutt 3068;* circa Cordoba, *Woronow 2947;* Rio Seco prope Cordoba, *Woronow 3038;* Cordoba, *Greenman 161;* barranca of Chevastl near Huatusco, *Rozynski 782.* DATA INCOMPLETE: *Sumichrast 882.*

The identity of *H. americanus* is based on the interpretations by E. G. Baker[8] and T. A. Sprague.[9]

This species has very characteristic ovate-lanceolate leaves, which are densely tomentose only on the lower surface.

9. Heliocarpus Donnell-Smithii Rose, in Bot. Gaz. 31:110. 1901. (T.: *J. D. Smith 1722*).

H. Caeciliae Loesener, in Fedde, Rep. Spec. Nov. 12:227. 1913. (T.: *Seler 4976*).
H. horridus Lundell, in Bull. Torr. Bot. Club 66:597. 1939. (T.: *Lundell & Lundell 7821*).
H. cuspidatus Lundell, in Phytologia 2:2. 1941. (T.: *Gentle 2297*).
H. floribundus Lundell, loc. cit. 1941. (T.: *Gentle 1534*).

Small trees about 10 m. high; older branches glabrous, smooth, yellow to yellowish brown, irregularly punctate with white lenticels; younger branches and inflorescence axes slightly pubescent with short stellate and simple hairs. Leaves broadly ovate, 12–14 cm. long and 8–10 cm. wide, not lobed, 5-costate at the base, shortly acuminate, base rounded or obtuse, irregularly serrated, lower serrations glandular, upper surface dark green, essentially glabrous with short greatly suppressed stellate hairs, lower surface lighter green, slightly more pubescent than the upper, nearly glabrate, with short stellate pubescence; petioles glabrous, smooth, 6–8 cm. long. Inflorescences gynodioecious, usually terminal, rarely axillary; the hermaphrodite large and spreading, about 18 cm. long and 15 cm. wide, the cymes of about 20 flowers, rather loose, the flowering peduncle mostly 3-radiate, rarely 2-radiate, 2 mm. long, the pedicels 4–5 mm. long, the buds obovoid, slightly constricted in the middle, not appendaged at the tips of the sepals, the sepals 4, linear, 4–6 mm. long and 1–2 mm. wide, light green with stellate pubescence without, glabrate, yellow to yellowish brown within, the petals 4, linear-spatulate, 3-nerved, slightly shorter than the sepals, about 4 mm. long, the stamens 12–16, with filaments about as long as the petals, the ovary ellipsoid, about 1–2 mm. long, borne upon a gynophore nearly as long or very slightly shorter than the ovary itself, with a style 3–4 mm. long, bifid about one quarter of its length and with stigma lobes acute, spreading; the pistillate greatly condensed and crowded, about 5 cm. long and 5 cm. wide, the cymes of about 20 flowers, crowded in nodose clusters, the flowering peduncles very short, 3-radiate, bearing 2 small bracteoles, the pedicels 1–2 mm. long, the buds about 2–3 mm. long, not appendaged at the tips of the sepals, the sepals 4, linear, 2–3 mm. long, light green and slightly pubescent without, generally brownish and glabrate within, the petals none, the staminodes none, the ovary suborbicular, about 1 mm. long, borne upon a very short gynophore shorter than the length of the ovary, with a style nearly twice the length of the ovary, very briefly bifid, the stigma lobes acute. The fruit ellipsoid, nearly glabrate at maturity, slightly rugose, 5 mm. long and 3 mm. wide, borne on a gynophore 8–12 mm. long, bearing 2–4 pairs of plumose bristles, the fringe of two rows of plumose bristles 5–7 mm. long; the seed obliquely ovoid, 2–3 mm. long and about 2 mm. wide, with a distinct groove in the middle.

Distribution: Plants of southern Mexico and Central America. This species is of rather wide continental distribution but its presence in Martinique is difficult to explain, unless through introduction. It is abundant on the edges of forest, in secondary growth, and on mountain slopes at altitudes from 100 to 1500 m. Flowers from December to February, and the fruits are persistent up to June.

Fig. 9. *H. Donnell-Smithii*

Map 9. Distribution of *H. Donnell-Smithii*

MEXICO: OAXACA: Tuxtepec, Chiltepec and vicinity, *Calderón 452.* QUINTANA ROO: Coba, *Lundell & Lundell 7821.* TABASCO: Atasta, *Rovirosa 120.* VERA CRUZ: Montzorongo, *J. G. Smith 234;* Wartenberg, near Tantoyuca, prov. Huasteca, *Ervendberg 225;* Santa Lucrecia, *Mell 670;* Coatzacoalcoa, isthmus of Tehuantepec, *C. L. Smith 1002;* district San Andres Tuxtla, Salto de Chilapan, *Seler 4976.*

BRITISH HONDURAS: Belize District, Gracie Rock, Sibun River, *Gentle 1534;* El Cayo District, Vaca, *Gentle 2207;* El Cayo District near Camp 6, *Gentle 2355;* Inacahual, Stann Creek District, Middlesex, *Gentle 2788;* Middlesex, *Stevenson 3336;* 22 Mile, alt. 200 ft., *Schipp 872.*

GUATEMALA: ALTA VERAPAZ: Arenal, alt. 3000 pp., *J. D. Smith 1722;* Savanna, north of Concepcion, 3–5 miles southeast of Finca Yalpemech, near Alta Verapaz-Peten boundary line, alt. 100–110 m., *Steyermark 45229;* southwest of Lanquin, alt. 600–1000 m., *Steyermark 44067, 44068;* Semacoch, trail to Panzas, *Goll 255;* road to Sepaciute, *Wilson 1978;* mountain slopes above Finca, Semay, *Wilson 198.* IZABAL: between Los Amates and Izabal, *Kellerman 6448.* SUCHITEPEQUEZ: Mazatenango, alt. 300 m., *Kellerman 6068.*

HONDURAS: ATLANTIDA: vicinity of Tela, alt. 20–600 m., *Standley 55518.*

NICARAGUA: MANAGUA: vicinity of Managua, *Garnier 560.* GRANADA: Volcán Mombacho, *Baker 2490.*

MARTINIQUE: bois près Fort de France, *Hahn 1340;* St. Pierre, *Curran 7.*

This species is characterized by its ellipsoid, nearly glabrate fruits borne on a long bristly gynophore, and by its ovate leaves, which are nearly blabrous to glabrate.

10. HELIOCARPUS POPAYANENSIS HBK. Nov. Gen. Sp. 5:341. 1821. (T.: *Humboldt & Bonpland, in Herb. Paris*).

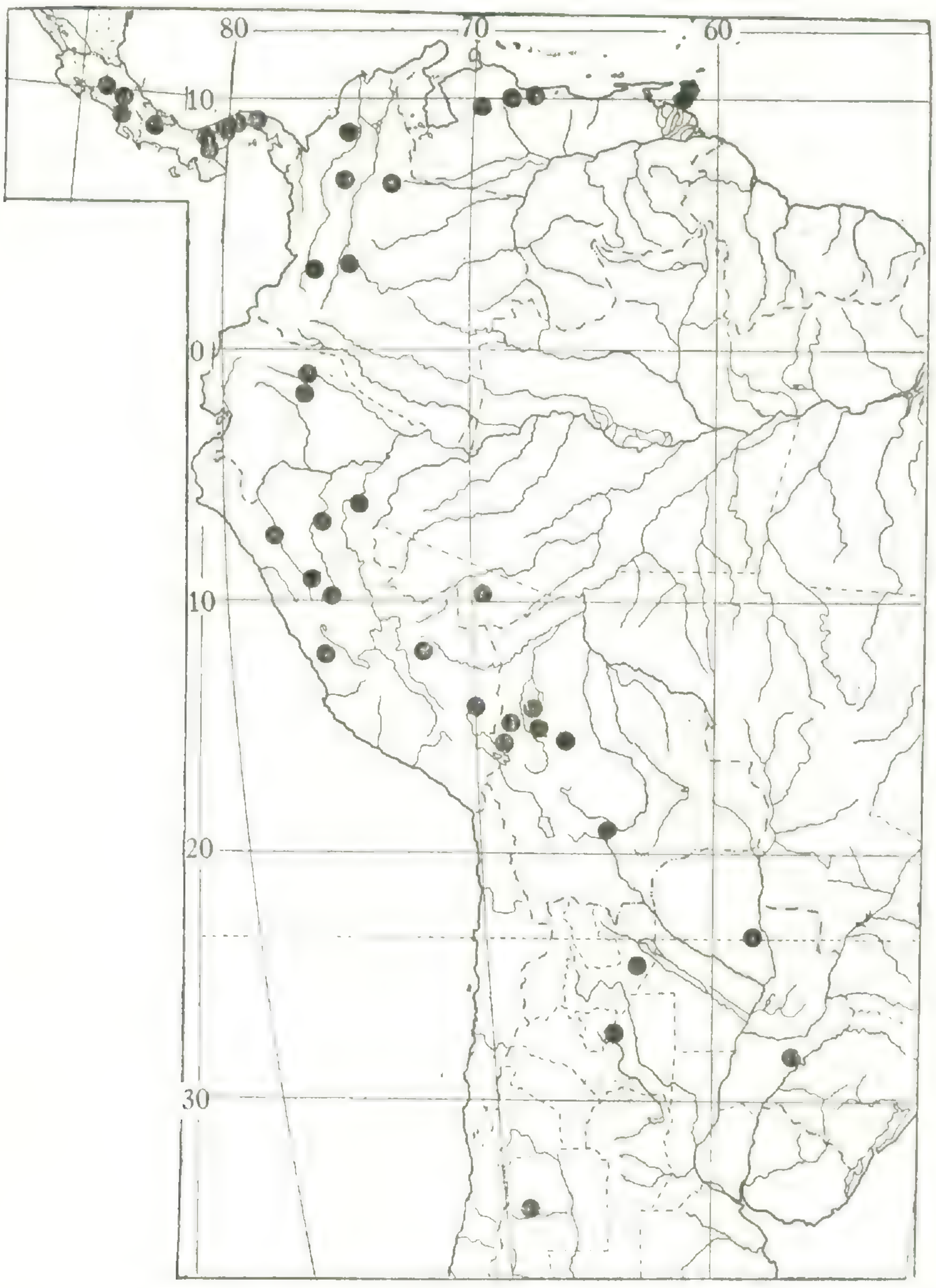
H. trichopodus Turcz. in Bull. Soc. Nat. Moscou 31^1:226. 1858. (T.: *Funck & Schlim 150*).
H. americanus var. *popayanensis* (HBK.) K. Schum., in Martius, Fl. Bras. 12^3:141. 1886.
H. popayanensis var. *Schumanni* E. G. Baker, in Jour. Bot. 36:132. 1898.
H. popayanensis var. *Purdiei* E. G. Baker, loc. cit. 1898.
H. popayanensis var. *trichopoda* (Turcz.) E. G. Baker, loc. cit. 1898.
H. popayanensis var. *grandifolius* Hochr. in Ann. Conserv. et Jard. Bot. Genève 18:116. 1914. (T.: *Bang 1455*).
H. diclinus Hochr. loc. cit. 117. 1914. (T.: *H. H. Smith 1908*).
H. boliviensis Hochr. loc. cit. 118. 1914. (T.: *Bang 1491*).
H. stipulatus Hochr. loc. cit. 121. 1914. (T.: *Poeppig 3102*).
H. Rosei Hochr. loc. cit. 119. 1914. (T.: *Bang 2305*).
H. americanus acc. to E. E. Wats. in Bull. Torr. Bot. Club 50:123. 1923, not L.
H. australis E. E. Wats. loc. cit. 124. 1923. (T.: *Hassler 557*).
H. rudis E. E. Wats. loc. cit. 126. 1923. (T.: *Pittier 3082*).
H. subtrilobus Sprague, in Bot. Gaz. 61:257. 1923. (T.: *Fendler 1277B*).

Trees usually about 8–10 m. high or more; older branches glabrate, slightly rugose, cream to brown, irregularly punctate with few, rather small, white lenticels; younger branches and sometimes a few of the older branches covered lightly with ferruginous tomentum of both stellate and long coarse simple hairs. Leaves usually 3-lobed with acuminate apices, but sometimes only obscurely so, about 16–20 cm. long and 14–18 cm. wide, base markedly cordate on mature leaves, younger leaves usually with rounded bases, irregularly serrated, upper surface generally dark green, glabrate with short ferruginous stellate tomentum, especially on the veins and veinlets, lower surface light green, slightly more pubescent than the upper, the

Fig. 10. *H. popayanensis*

pubescence varying from densely stellate to thinly suppressed stellate, the principal veins usually with simple hairs about 2 mm. long; petioles 6–8 cm. long, usually densely covered with both stellate and simple hairs. Inflorescences gynodioecious, usually terminal; the hermaphrodite about 12 cm. long and 14 cm. wide, the cymes of about 12–16 flowers, the flowering peduncles 3-radiate, about 1–2 mm. long, the pedicels about 2–3 mm. long, the buds obovoid, slightly constricted towards the base, without appendages at the tips of the sepals, the sepals 4, spatulate, generally 3-nerved, about 5 mm. long, light green and densely tomentose without, glabrate and yellowish brown within, the petals 4, spatulate, about 3–4 mm. long, slightly ciliate, the stamens about 12–16, with the filaments about 3–4 mm. long, the ovary suborbicular, laterally compressed, about 1.0–1.25 mm. long, borne on a gynophore about 0.75 mm. long, with a style about twice the length of the ovary, bifid about one quarter of its length and with the stigma lobes spreading, each with 3 acute lobes; the pistillate rather large, much larger than the hermaphrodite, about 14 cm. long and 20 cm. wide, the cymes of 12–16 flowers, rather condensed in nodose clusters, the flowering peduncles 3-radiate, less than 1 mm. long, the pedicels about 1 mm. long, the buds about 3 mm. long, the sepals 4, linear, about 3 mm. long, light green, stellate-tomentose without, glabrate, cream to light brown within, the petals none, the staminodes about 12, the ovary suborbicular, about 1 mm. long, borne on a short gynophore, with a style about twice the length of the ovary, bifid about one quarter of its length and with spreading stigma lobes, each with 3 acute lobes. The fruit ellipsoid to ovoid, with many short tufts of stellate hairs, slightly pubescent, about 5–6 mm. long and 2–3 mm. wide, borne on a bristly gynophore about 1.0–1.5 mm. long with 2–3 pairs of plumose bristles, the fringe of two rows of plumose bristles about 8–12 mm. long; the seed ovoid, about 2 mm. long, with a shallow depression in the middle.

Distribution: A species which extends from Costa Rica to northern Argentina. It is primarily South American and is the only species known there. In southern Central America and northern South America it is found in highlands above 1000 m. altitude, while in Paraguay and Argentina it is usually at lower elevations. *H. popayanensis* frequents steep slopes in forested river valleys, thickets, or in sunny bushy slopes, usually in second growth in cut-over forests. It is abundant in rain or cloud forests or on the edges of forests at stream sides. Flowers in its northern



Map 10. Distribution of *H. popayanensis*

range from December to January and in its southern range from May to June. Fruits persistent in the north until about the middle of March and in the south to about the end of September.

COSTA RICA: ALAJUELA: hills west of Zapate, San Carlos, alt. 1550 m., *A. Smith NY1263;* Zacero, upper continental divide, alt. 1800 m., *A. Smith H1358.* HEREDIA: Vera Blanca de Sapiqui, near slope of Central Cordillera, between Poas and Barba volcanoes, alt. 1680 m., *Skutch 3346.* SAN JOSÉ: La Palma de San Ramon, *Brenez 6369;* Carpintera, alt. 5700 ft., *Stork 1158.* DATA INCOMPLETE: Charco, Goicochea, alt. 1400 m., *Jimenez 993.*

PANAMA: CANAL ZONE: Cerro Gordo, near Culebra, alt. 50–290 m., *Pittier 2305;* Barro Colorado Island, *Frost 218;* Canal Zone and vicinity, C.16, back of Curundu, *Harvey 5258;* Barro Colorado Island, *Shattuck 662, 754;* near lab., Barro Colorado Island,

Woodworth & Vestal 730, 748; Barro Colorado Island, *Wetmore & Abbe 108;* Empire Station, *Hayes 437.* CHIRIQUÍ: valley of the upper Río Chiriquí Viejo, *White 29;* around Camp Aguacatal, eastern slope of Chiriquí Volcano, alt. 2100–2200 m., *Pittier 3082;* vicinity of "New Switzerland" central valley of Río Chiriquí Viejo, alt. 1800–2000 m., *Allen 1398;* vicinity of Cerro Punta, alt. 2000 m., *Allen 1519.* COCLÉ: hills south of El Valle de Antón, alt. 600–800 m., *Allen 2849, 2912;* El Valle de Antón, alt. 600–800 m., *Hunter & Allen 304.* DARIÉN: locality not mentioned, *Macbride 2713.*

TRINIDAD: St. Ann's Cascade, *Broadway 6569;* Santa Cruz, *Simmonds 281;* Lady Chancellor Road, St. Ann's, *Broadway 9200;* Knagg's Hill, *R. O. Williams 12671;* St. Cruz, *collector unknown 649, 650.*

COLOMBIA: ANTIOQUIA: vicinity of Medellin, *Toro 206.* BOYACA: 130 m. n. of Bogota, El Umbo, alt. 3700 ft., *Lawrance 590.* CAUCA: El Tambo in silva, alt. 1700 m., *Sneidern 434;* highlands of Popayan, alt. 1400–2000 m., *Lehmann 5502;* Río Toribio region, alt. 100–1200 m., *Espiña & Giacometto 20861;* cerca de Popayan, matorrales en Río Blanco, alt. 1800 m., *Arbelaez & Cuatrecasas 5798.* MAGDALENA: Santa Marta, alt. 2000 ft., *H. H. Smith 1908;* Pita, *André 467.* NARINO: frontera Colombo-ecuatoriana, selva higrofila del Río San Miguel, junto a la desembo-cadure del Río Conejo, alt. 300 m., *Cuatrecasas 10925.* NORTE DE SANTANDER: Cordillera Oriental, region del Sarare, Quebrada de la China (en la Hoya del Cubugon), Santa Librada en El Reposo, alt. 800 m., *Cuatrecasas 13262, 13340;* Cordillera Oriental, region del Sarare, Hoya del Río Chitaga entre Chorro Colorado y Bata, alt. 1300 m., *Cuatrecasas, Schultes & Smith 12237;* Cordillera Oriental, region del Sarare, La Cabuya, alt. 1300 m., *Cuatrecasas, Schultes & Smith 12590;* Cordillera Oriental, region del Sarare, entre el Alto del Loro y el Alto de Santa Ines, bosques, alt. 1800–2000 m., *Cuatrecasas, Schultes & Smith 12471.*

VENEZUELA: DISTRITO FEDERAL: Caracas, alt. 3000 pp., *Funck & Schlim 150;* Carteza, alt. 930 m., *L. Williams 9957.* MERIDA: prope coloniam Tovar, *Fendler 1277, 1277B.* MIRANDA: La Malva, near Las Mostazas, *Allart 273;* La Malva, cerca de las Mostazas, *Pittier 273;* in valley from El Valle to Cua, *Pittier 11975;* en matorrales a lo largo de la carretera de los Teques, alt. 1200 m., *L. Williams 10692.* YARACUY: Hacienda Iboa near San Pablo, *Pittier 12605.* DATA INCOMPLETE: Las Trincheras, *Warming 313;* al sur de Río Claro, alt. 1360 m., *Saer 778.*

BRAZIL: ACRE: near mouth of Río Macauhan (tributary of Río Yaco), lat. 9.20′ S., and long. 69. W., *Krukoff 5261.*

ECUADOR: AZUAY: along Río Patul between Hacienda Yubay and Hacienda San José de Caimotan, in region of Sanaguin, alt. 850 m., *Steyermark 52754;* Hacienda Yubay, at Sanaguin, on south side of Río Patul, alt. 850 m., *Steyermark 52694;* Río Norcay between Río Gamolotal and Río Norcay, alt. 1095–1370 m., *Steyermark 52878.* CHIMBORAZO: Chimbo, alt. 1000 m., *Rimbach 288.* DATA INCOMPLETE: vicinity of Ventura, *Rose & Rose 23518.*

PERU: CAJAMARCA: Guerocotillo, Prov. Contervo, alt. 2000 m., *Weberbauer 7124.* CUZCO: Río Chaupimayo, Convencion, *Soukup 790.* HUANUCO: Monzon, alt. 900–1000 m., *Weberbauer 3432;* Cueva Grande, estacion near Pozuzo, alt. 3500 ft., *Macbride 4765;* Vinyyacu, *Sawada 101.* JUNIN: Chanchamayo Valley, alt. 1500 m., *Schunke 290, 293;* Pichis Trail, Dos de Mayo, alt. 1700–1900 m., *Killip & Smith 25864.* LORETO: Muna, *Macbride 4065;* lower Río Huallaga, alt. 155–210 m., *Klug 3076;* west of Tarapota, *Spruce 4558.* SAN MARTIN: Juan Jui, alto Río Huallaga, alt. 400–800 m., *Klug 4395.* DATA INCOMPLETE: *Poeppig 1894, 3102; Ruiz & Pavon 39/8, 39/9.*

BOLIVIA: COCHABAMBA: Incachaca—S. Antonio, alt. 1500 m., *Werdermann 2126.* LA PAZ: Calapampa, Coroico, *Bang 2305;* Mapiri, *Bang 1491;* Guanai-Tipuani, *Bang 1455;* Guanai, alt. 2000 ft., *Rusby 1492;* Beni River, *Rusby 1493;* Moryungas, Region von Coripata, Hacienda "El Choro", *Buchtien 8125;* Province of S. Yungas, basin of Río Bopi, San Bartoloma (near Calisaya), alt. 750–900 m., *Krukoff 10249, 10283, 10409.* SANTA CRUZ: Legunillas, Cordillera of Tecahuasi, alt. 1600 m., *Cardenas 2839.*

ARGENTINA: CATAMARCA: Del Alto, Bategua, alt. 1250 m., *Venturi 7074.* MISIONES: vicinity of Puerto Aguirre, alt. 100 m., *Curran 9, 17;* vicinity of Puerto Leon, alt. 75–100 m., *Curran 700, 718.* TUCUMAN: Famailla, San Pablo, alt. 600 m., *Venturi 1002, 1002C;*

Famailla, San Rafael, *Venturi 9205;* locality not mentioned, *Hauman 9206.*
HAWAII: Oahu, planted in foothills for reforestation, *Degener 10843.*

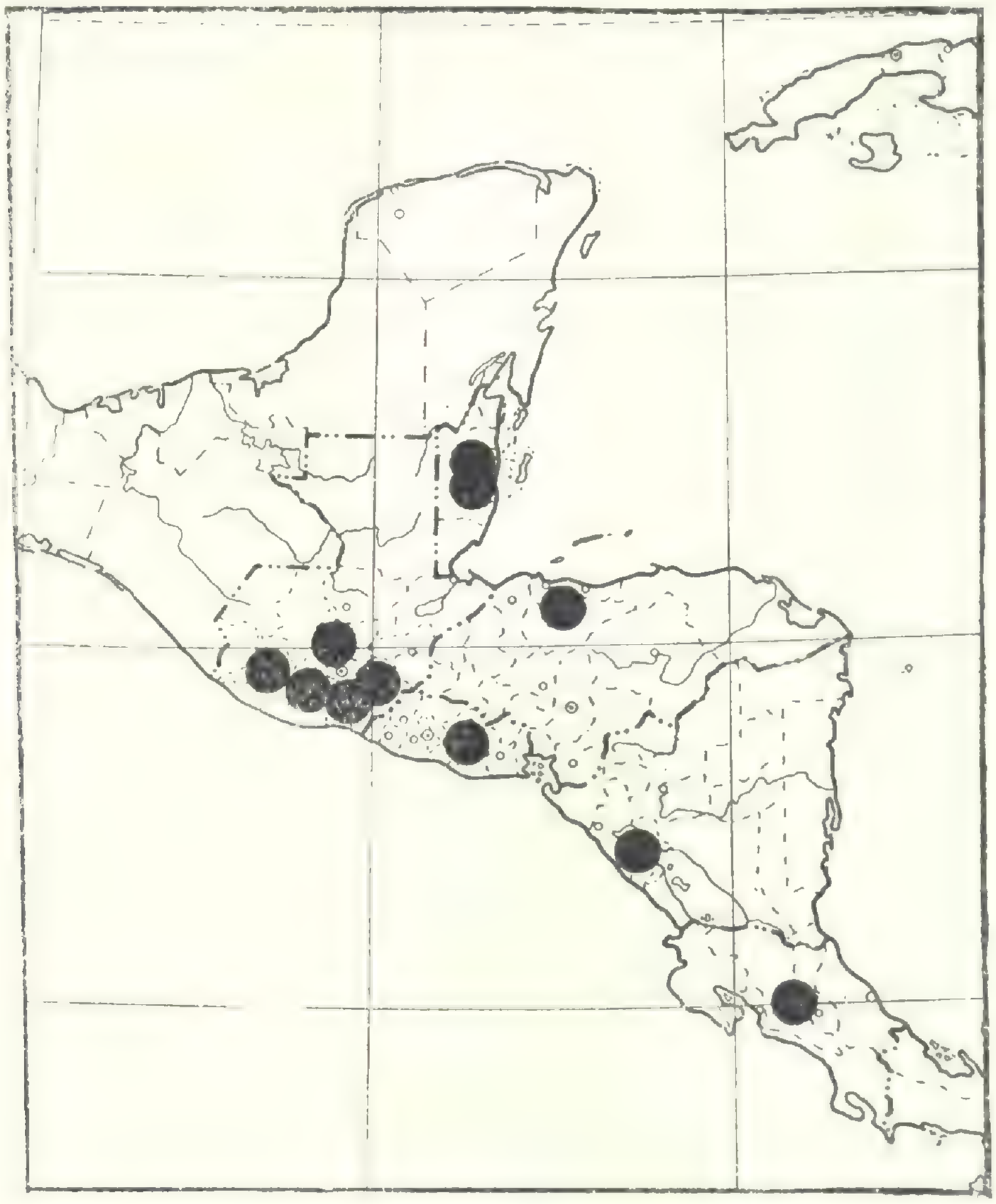
The plants of this species have leaves whose diversity of shape and size is unparalleled in the whole genus. A general tendency is for the plants in the central range of the species to have leaves more definitely and acutely 3-lobed than those towards either the northern or the southern limits, where the leaves frequently may be quite undivided. The pubescence varies from slightly tomentose to nearly glabrate. The constant characters throughout its wide distribution are the hirsute induments on the lower nerves, the sepals without appendages, the 3-parted stigma lobes, and the fruits, which are ellipsoid to ovoid and slightly tomentose.

11. HELIOCARPUS NODIFLORUS (Donn. Sm.) Donn. Sm. & Rose, in Contr. U. S. Nat. Herb. 5:126. 1897.

H. polyandrus var. *nodiflorus* Donn. Sm. in Bot. Gaz. 23:240. 1897. (T.: *Heyde & Lux 4329*).
H. excelsior Morton, in Jour. Wash. Acad. Sci. 27:307. 1937. (T.: *Skutch 2250*).
H. Gentlei Lundell, in Phytologia 2:2. 1941. (T.: *Gentle 1787*).

Fig. 11. *H. nodiflorus*

Trees about 10–18 m. high; older branches glabrate, longitudinally ridged, light brown, punctate irregularly with few white lenticels; younger branches and inflorescence axes scurfy, slightly ferruginous-pubescent with both simple and stellate hairs. Leaves 3-lobed, sometimes obscurely so, generally medianly oblique, large, 16–18 cm. long and 15–18 cm. wide, 5- to 7-costate at the base, acute to



Map 11. Distribution of *H. nodiflorus*

acuminate, base usually cordate, sometimes slightly rounded, rather regularly and doubly serrated, lower serrations slightly glandular, upper surface dark green, glabrate, with few tufts of short stellate hairs in the nerve axes, lower surface light green, slightly more pubescent than the upper, especially in the nerve axes; petioles large and stout, about 10 cm. long, lightly ferruginous-stellate-pubescent, scurfy; stipules sometimes persistent. Inflorescences gynodioecious, usually terminal, large and spreading; the hermaphrodite about 15 cm. long and 18 cm. wide, the cymes of about 15–20 flowers borne in compact nodose clusters, the flowering peduncles 3-radiate, about 2 mm. long, the pedicels 1–3 mm. long; the buds obovoid, slightly constricted in the middle towards the base, sometimes with small acute appendages on the tips of the sepals, the sepals 4, spatulate, 4–5 mm. long, light green with stellate tomentum without, glabrate and yellowish brown within, the petals 4, linear, 1-nerved, about 4 mm. long, the stamens about 20–24, with the filaments about 4 mm. long, the ovary ovoid, slightly compressed, about 1.5 mm. long, borne on a short gynophore less than 1 mm. long, with a style about 3–4 mm. long, bifid about half its length at anthesis and with the stigma lobes acute and spreading; the

pistillate about as large as the hermaphrodite, the cymes of about 20 flowers, rather compressed and crowded in nodose clusters, the flowering peduncles 3-radiate, less than 1 mm. long, the pedicels about 1–2 cm. long, the buds about 2–3 mm. long, usually not appendaged at the tips of the sepals, the sepals 4, linear, about 2–3 mm. long, light green and stellate-pubescent without, glabrate and yellowish brown within, the petals none, the staminodes about 12–16 or none, the ovary ovoid, small, about 1 mm. long, slightly compressed, borne on a short gynophore, with a style slightly longer than the ovary, briefly bifid and with the stigma lobes acute. Fruit orbicular, slightly tomentose with short separate tufts of stellate hairs, about 5–6 mm. in diameter, borne on a bristly gynophore 10–15 mm. long, bearing 2–3 pairs of plumose bristles, the fringe of 1 or 2 rows of plumose bristles 6–8 mm. long; the seed obliquely ovoid, about 2–3 mm. long, with a distinct groove in the middle.

Distribution: A species primarily of Central America, extending into southeastern Mexico. It is common in clearings and in wet thickets, nearly always in secondary growth besides rivers or in sheltered valleys, usually at altitudes from 1000 to 2500 m. Flowers from January to February, the fruits persisting until about the middle of April.

BRITISH HONDURAS: Gracie Rock, Sibun River, *Gentle 1787;* Stann Creek Valley, 17 miles, *Gentle 3202, 3203, 3204;* Stann Creek Valley, Big Eddy Creek, *Gentle 3470;* Little Cocquericot, Belize River, *Lundell 4177.*

GUATEMALA: CHIMALTENANGO: lower and middle southwestern slopes of Volcán Fuego, above Finca Montevideo, along barranco Espinazo and tributary of Río Pantaleon, alt. 1200–1600 m., *Steyermark 52113.* EL PROGRESO: Montana Canahui, between Finca San Miguel and summit of mountain, near upper limits of Finca Caieta, alt. 1600–2300 m., *Steyermark 43825.* ESCUITLA: between Río Jute and Río Pantaleon, on road between Escuintla and Santa Lucia Cotz, alt. 540–720 m., *Standley 63443.* QUEZALTENANGO: Pueblo Nuevo, alt. 500–600 m., *Steyermark 35467;* Colomba, alt. 3000 ft., *Skutch 2037.* QUICHE: Nebaj, alt. up to 6200 ft., *Skutch 1763.* SAN MARCOS: between Rodeo and Malacate, alt. 1400–3500 ft., *Nelson 3742.* SANTA ROSA: Río Pinula, alt. 4000 pp., *Heyde & Lux 4329;* Naranjo, alt. 1100 m., *Heyde & Lux 4177.*

HONDURAS: ATLANTIDA: Lancetilla Valley, near Tela, alt. 20–600 m., *Standley 53854, 55791, 55793, 56640.*

NICARAGUA: GRANADA: Mombacho, *Oersted 14829.*

COSTA RICA: SAN JOSÉ: vicinity of El General, alt. 640–1100 m., *Skutch 2250, 2266, 3820, 3852.*

It is unfortunate that the type of *H. nodiflorus (Heyde & Lux 4329)* has flowers with small apical appendages. The appendages in this species actually are rarely present, and if present are extremely small. This species is characterized by its large leaves, the largest known for the genus, which are nearly glabrous on both the surfaces. The fruit is like that of *H. Donnell-Smithii,* but is more spheroid, slightly more tomentose, and larger in size. It can be distinguished from *H. popayanensis* by its large orbicular fruits, as well as by its glabrous leaves.

INDEX TO EXSICCATAE

Italicized numerals refer to collector's numbers, *s. n. (sine numero)* to unnumbered collections; parenthetical numerals refer to the numerals of taxonomic entities conserved in this revision.

Aguilar, I. *81*(6); *97100*(7).
Allart, A. *273*, *516*(10).
Allen, P. H. *641*, *1398*, *1519*, *2849*, *2912* (10).
André, E. *467*, *800*, *K. 924*, *K. 925*(10).
Arbelaez, E. P. & Cuatrecasas, J. *5798* (10).
Ariste-Joseph, Bro. *A. 370*(10).
Baker, C. F. *2490*(10).
Balansa, B. *2295*(10).
Bang, M. *1455*, *1491*, *2305*(10).
Barnes, C. R. & Land, W. G. *285*(1).
Berlandier, J. L. *1064*(1); *971*(2).
Brandegee, T. S. *s. n.*(3).
Brenes, A. *655*(7); *6369*(10).
Botteri, —. *340*, *341*, *882*, *888*, *992*(8).
Bourgeau, M. *1200*(1); *1574*, *1819*, *1875*, *1974*(8).
Britton, N. L. & Broadway, W. E. *467* (10).
Broadway, W. E. *5199*, *6569*, *9200*(10).
Buchtien, O. *8125*(10).
Calderón, G. M. *452*(9).
Cardenas, M. *2839*(10).
Christopherson, E. D. *117*(10).
Collins, G. N. & Doyle, C. B. *252*, *255*(7).
Conzatti, C. *s. n.*, *4313*(1); *1694*(8).
Cook, O. F. & Griggs, R. F. *204*, *722*(7).
Cowell, J. F. *270*, *271*(10).
Cuatrecasas, J. *10925*, *13262*, *13340*(10).
Cuatrecasas, J., Schultes, R. E. & Smith, E. *12237*, *12471*, *12590*(10).
Cumming, H. *1131*(10).
Curran, H. M. *7*(9); *9*, *17*, *700*, *718*(10).
Daniel, Bro. *1024*(10).
Dayton, W. A. *3156*(7).
Degener, O. *10843*(10).
Dodge, C. W., Hanckel, R. & Thomas, W. S. *6379*(7).
Edwards, J. B. *465*(11).
Emrick, G. M. *192*(5).
Englesing, F. C. *136*, *140*(7).
Ervendberg, L. C. *225*(9).
Espiña, —. & Giacometto, —. *20861*(10).
Fendler, A. *1277*, *1277B*(10).
Ferris, R. S. *6025*(5).
Fiebrig, K. *2a*(10).
Fröderström, H. & Hulten, E. *860*(8); *780*(9).
Frost, S. W. *218*(10).
Funck & Schlim *150*(10).
Galeotti, H. *4154*(6); *4162*, *4162B*(8).
Garnier, A. *560*(9).
Gaumer, G. F. *1234*, *1315*, *2275*, *2302*, *23488*, *24177*(6).
Gentle, P. H. *2273*(6); *1534*, *2297*, *2355*, *2788*, *3203*(9); *1787*, *3204*, *3470*(11).
Gentry, H. S. *1644*, *1709*, *2440*, *5069*, *6607*(3); *4792*(4).
Ghiesbreght, M. *51*(6).
Goldman, E. A. *226*(3); *70*(8); *37*(9).
Goll, G. P. *255*(9).
Gonzalez, J. *860*(4).
Greenman, J. M. *161*(8).
Haenke, T. *2468*(2).
Hagen, C. von & Hagen, W. von. *107* (7); *1010*, *1070*, *1224*(11).
Hahn, L. *1340*(9).
Halbinger, C. *61*(1).
Hancock, W. *12*(5).
Harvey, D. R. *5258*(10).
Hassler, E. *557*, *557a*, *11856*(10).
Hauman, —. *9206*(10).
Hayes, S. *437*, *947*, *1015*(10).
Heyde, E. T. *381*(6); *637*, *658*(11).
Heyde, E. T. & Lux, E. *3956*(6); *4177*, *4329*(11).
Hinton, G. B. *2723*, *4953*, *5119*, *6736*, *7077*, *12449*, *12477*, *13246*, *14831*(1); *2843*, *5109*, *5369*, *5416*, *7036*, *7155*, *7236*, *7243*, *13398*(2); *4265*, *6605*, *6621*, *6724*, *6876*, *6901*, *6905*, *6906*, *9801*, *9802*, *10901*(5).
Holton, I. F. *770*(10).
Hunter, A. A. & Allen, P. H. *304*(10).
Jack, J. G. *8689*(10).
Jimenez, D. *993*(10).
Johnston, J. R. *1106*, *1332*(6).
Jones, M. E. *27153*, *97400*(1).
Jorgenson, P. *4500*(10).
Juzepczuk, —. *1461*(1).
Kellerman, W. A. *6068*, *6448*(9).
Kerber, E. *276*, *483*(8).
Killip, E. P. *8248*(10).
Killip, E. P. & Smith, A. C. *15009*, *15518*, *19481*, *25864*(10).
Klug, C. *3076*, *3627*, *4395*(10).
Krukoff, B. A. *5261*, *10249*, *10283*, *10409* (10).
Langlassé, E. *572*(1); *623*(5).
Lawrance, A. E. *590*(10).

Leavenworth, W. C. & Hoogstraal, H. *1731, 1525*(5).
Lehmann, F. C. *B.T. 553, 5502*(10).
Lemmon, J. G. & Lemmon, —. *s. n., 251* (1).
LeSueur, H. *1404*(3); *661, 1158*(4).
Lévy, P. *483*(7).
Liebmann, F. M. *473*(1); *522, 523*(6); *477*(7); *471, 475, 478* (8).
Linden, J. *858, 898*(6); *1609*(7); *857* (8).
Lundell, C. L. *959, 1192*(6); *4177, 6516* (11).
Lundell, C. L. & A. A. Lundell *7821*(9).
Lyonnet, E. *1178*(1); *1190, 1726*(2).
MacBride, J. F. *2713, 4065, 4765*(10).
Martinez, M. *s. n., 110*(1); *222*(8).
Maxon, W. R. *4751*(10).
Maxon, W. R. & Hay, R. *3156*(6); *3305, 3306, 3322*(7).
Medellin, R. *92*(8).
Mell, C. D. *670*(9).
Mexia, Y. *809*(1); *1100*(2); *7141*(10).
Miguel, H. A. *105*(10).
Morales, J. *1.122*(6).
Muller, C. H. *3634*(4).
Müller, F. *884, 1037, 1049*(8).
Mutis, J. C. *1474, 1478, 3921, 4383*(10).
Narvaez-Montes, M. & Salazar, A. E. *860* (4).
Nelson, E. W. *1243, 1485, 1818, 3520, 7046*(1); *2298, 6970*(2); *3400*(6); *4383* (7); *70, 119*(8).
Orcutt, C. R. *4463, 4465*(5); *3068*(8).
Ortega, J. G. *3087*(3); *3130, 4612*(4).
Ostenfeld, C. H. *50*(10).
Palmer, E. *157*(2); *97, 100, 191, 629*(3); *99, 647, 732, 733*(4); *440, 986*(5).
Pennell, F. W. & Killip, E. P. *6337, 8097* (10).
Piper, C. V. *5532, 5612*(10).
Pittier, H. *13022*(6); *273, 2305, 3082, 5392, 11975, 12605, 13022*(10).
Poeppig, E. *1894, 3102, 3627*(10).
Pringle, C. G. *1791, 8227, 8719, 9692, 9693*(1); *8694*(2); *10069*(5); *6106*(8).
Purpus, C. A. *3062*(1); *7524*(2); *2227, 15704a*(6); *2226, 2387, 8275*(8).
Record, S. J. & Kuylen, H. *H. 25, G. 99* (6); *9958*(7); *10034*(8).
Reed, E. *440*(10).
Regnell, A. F. *III 285*(10).
Reko, B. P. *4448, 4571*(1).
Renson, C. *61*(6).
Rimbach, A. *288*(10).
Rodriguez, J. V. *1679*(6).
Rojas, S. *534*(7).
Rose, J. N. *2305, 2496, 3090*(1); *1694* (3); *2860a, 2860b*(5).
Rose, J. N. & Hough, W. *4335, 4565, 4828*(1); *4314*(7); *4304*(8).
Rose, J. N. & Painter, J. H. *7390, 7537, 7646*(1); *7389*(5).
Rose, J. N. & Rose, G. *23518*(10).
Rose, J. N., Standley, P. C. & Russell, P. G. *12828*(4).
Rovirosa, J. N. *120*(9).
Rowlee, W. W. & Rowlee, H. E. *212*(7).
Rozynski, K. *782*(8).
Ruiz, H. & Pavon, J. *39/8, 39/9*(10).
Rusby, H. H. *1492, 1493*(10).
Saer, J. *778*(10).
Sivon, M. *503*(1).
Sawada, M. *101*(10).
Schipp, W. A. S. *580*(6); *872*(9).
Schunke, C. *200, 203*(10).
Seler, C. & E. *4196, 4829*(1); *5381*(2); *3766*(8); *4976*(9).
Shattuck, O. *662, 754*(10).
Simmonds, N. W. *281*(10).
Skutch, A. F. *3922, 4226*(7); *3346*(10); *1445, 1763, 2037, 2250, 2266, 3820, 3852*(11).
Smith, A. *H 1358, Ny. 1263*(10).
Smith, C. L. *1002*(9).
Smith, H. H. *1908*(10).
Smith, J. D. *1723*(7); *1722*(9).
Smith, J. G. *284*(8); *234*(9).
Smith, L. C. *797, 939*(1).
Sneidern, K. von. *434, 1431*(10).
Solis Rojas, F. *354*(7).
Soukup, J. *790*(10).
Spruce, R. *4558*(10).
Standley, P. C. *19303, 19660, 20304, 59888, 64273, 78068, 80064, 81067*(6); *54096*(7); *55149, 55154, 55518*(9); *31552*(10); *53854, 55791, 55793, 56640, 63443, 88541*(11).
Standley, P. C. & Valerio, J. *44633, 45148* (7); *44147*(10).
Stevenson, N. S. *336*(9).
Steyermark, J. A. *30577, 31912, 44076, 52218*(6); *44342, 45229, 48987, 49169* (7); *44067, 44068, 45229*(9); *52694, 52754, 52878*(10); *35467, 43825, 52113* (11).
Stork, —. *1158*(10).
Sumichrast, —. *882*(8).
Tate, R. *31(384)*(7).
Thieme, C. *5160*(10).
Tonduz, A. *7451, 8453, 14828*(6); *8561* (7).

Toro, R. A. *206, 784, 846, 887*(10).
Triana, J. *s. n., 5367*(10).
Tuerckheim, H. von *7828, 8500*(7).
Urbina, —. *639*(1).
Velasco, L. V. *8997*(6).
Venturi, S. *1002, 1002c, 7074, 9205*(10).
Vogl, P. C. *50a*(10).
Warmings, E. *313*(10).
Weberbauer, A. *3432, 7124*(10).
Werdermann, E. *2126*(10).
Wetmore, R. H. & Abbe, E. C. *108*(10).
White, P. *29*(10).
Williams, L. *8273, 8288, 8289, 8400, 8526, 8527*(7); *4297, 9957, 10692*(10).
Williams, R. O. *649, 650, 12671*(10).
Williams, R. S. *827*(10).
Wilson, C. L. *197, 198*(9).
Woodworth, R. H. & Vestal, P. A. *730, 748*(10).
Woronow, G. *2333*(1); *2963*(7); *2947, 3038*(8).

NEW APOCYNACEAE OF SOUTH AMERICA

DAVID DE AZUMBUJA[1]
AND ROBERT E. WOODSON, JR.

SECONDATIA **Adolphii** Azambuja, spec. nov. Frutex altissime scandens lactescens; ramulis crassiusculis glabris in maturitate conspicue lenticellatis. Folia ovato-elliptica vel lanceolata basi rotundata vel obtusa apice anguste acuminata saepe mucronata 5–8 cm. longa 2.0–4.5 cm. lata firme membranacea vel leviter coriacea glabra supra nitidula subtus opaca ibique albida et tenuissime reticulata; petiolis 0.6–0.7 cm. longis. Inflorescentia terminalis laxe cymosa pauciflora folia subtendentia paulo superans; pedicellis 0.7–1.1 cm. longis glabris; bracteis minimis. Calycis laciniae ovato-triangulares acutae 2.5–3.0 mm. longae intus cum squamis parvis longis. Corolla salverformis tubo 6–7 mm. longo in regione staminium insertionis leviter dilatato intus puberulente lobis oblongo-linearibus vel lineari-lanceolatis obliquis 15–17 mm. longis glabris patentibus. Stamina prope basim tubi corollae inserta; antheris oblongo-sagittatis 3.5–4.0 mm. longis dorso puberulentis. Ovarium rotundatum 1.2–1.5 mm. altum minute puberulentum; stigmate 1.2 mm. alto subsessili basi dilatato ubique duos annulos superpositos efformat; disco annulare ovario multo minore. Folliculi fusiformi compressi et prope basim maxime dilatati apicem versus gradatim angustati lignosi striati 19–20 cm. longi ca. 3.5 cm. lati; seminibus oblongo-ellipticis coma e fasciculis pilorum opacorum argentorum reflexorum.—BRAZIL: AMAZONAS: Manaus, matas de terras altas a nordeste de Flores, Sept. 14, 1945, *A. Ducke 1,758* (fl.); same locality, Aug. 29, 1947, *A. Ducke 2,105* (fr.), in Herb. Jard. Rio de Janeiro *no. 60,224*.

This species is dedicated to my friend Dr. Adolpho Ducke. Although similar to *S. Duckei* in habit, the flowers of *S. Adolphii* are shorter than those of the latter because of the difference in size of the corolla lobes.

LACMELLEA **speciosa** Woodson, spec. nov. Arbores. Folia opposita breviter petiolata late oblonga acuta basi obtusa 14–18 cm. longa 5.5–8.0 cm. lata coriacea glabra; petiolis 7–8 mm. longis. Inflorescentia ut videtur terminalis sed versimiliter in axillis foliorum superiorum lateralis; pedunculo 5–7 mm. longo, bracteis ovatis minimis; floribus speciosis albidis subsessilibus. Corollae salverformis tubum ca. 3 cm. longum, faucibus paulo ampliatis ca. 5 mm. longis; lobis ca. 1.3 cm. longis 4 mm. latis. Calycis laciniae late subreniformes rotundatae ca. 2 mm. longae piloso-ciliatae. Antherae lineares 4 mm. longae. Pistillum 1 cm. longum in ovario gradatim ampliatum; stigmate ca. 2 mm. longo. Fructus ca. 3.5 cm. diam. lutei; seminibus 2.—COLOMBIA: DEL VALLE: Río Calima (region del Choco), La Trojita, 5–50 m. alt., Feb. 19–March 10, 1944, *J. Cuatrecasas 16568*, in Herb. Missouri Bot. Gard., HOLOTYPE.

---

[1] Agrônomo Silvicultor, Forest Service, Brazil.

Issued November 30, 1949.

This species is particularly noteworthy because of the corolla lobes which are much longer than those of any other known species of the genus. Since the lobes are nearly thrice the length of the corolla throat, a redefinition of Markgraf's (Notizbl. 15:618–619. 1941) sections EULACMELLEA and ZSCHOKKEA is required. Less satisfactory would be the erection of a third section to accommodate *L. speciosa*, merely on the basis of corolla proportions.

MALOUETIA **parvifolia** Woodson, spec. nov. Arbores graciles vel fructices lactescentes ca. 4–5 m. alti; ramulis gracilibus cortice nigris. Folia opposita brevissime petiolata late ovato-elliptica 4.5–5.5 cm. longa 2–3 cm. lata late obtusa basi obtusa vel rotundata subcoriacea glabra subtus cum domatiis parvis; petiolis 0.2–0.3 cm. longa. Inflorescentiae axillares pauciflorae subsessiles. Flores parvi albi; pedicellis cum pedunculo petiolos subaequantibus. Corollae salverformes tubo cylindrico 5-gono ca. 0.4 cm. longo basi ca. 0.1 cm. diam. extus glabro, lobis oblique lanceolatis acuminatis 0.8–0.9 cm. longis valde patulis intus papillatis. Calycis laciniae valde imbricatae late ovatae scariaceae ca. 0.2 cm. longae cum squamellis internis marginalibus solitariis. Antherae paene inclusae anguste lanceolato-sagittatae ca. 0.3 cm. longae dorso apicem versus sparse pilosulae. Ovaria ca. 0.5 mm. longa puberulo-papillata cum nectariis 5 fere aequilongis; stigmate fusiformi ca. 1 mm. longo cum stylo aequilongo. Folliculi lineari-fusiformi 6–9 cm. longi ca. 0.3 cm. crassi glabri; seminibus 2.5 cm. longis valde canaliculatis sparse pilosis.—VENEZUELA: AMAZONAS: aquatico, en las margenes abiertas y completamente inundadas cerca de la boca del Río Sanariapo, arriba de Raudal de Maipures, alt. 120 m., Feb. 7, 1942, *L. Williams 15968*, in Herb. Missouri Bot. Gard., HOLOTYPE.

This species, like that immediately preceding, was received from the U. S. National Herbarium a few years ago in an exchange of unnamed duplicates. *M. parvifolia* apparently is most closely allied to *M. cestroides*, of the *Robbia*-complex, but differs from it quantitatively in almost every detail.

MALOUETIA **grandiflora** Woodson, spec. nov. Arbores lactescentes ca. 8 m. altae; trunco ca. 12 cm. diam., ramulis gracilibus cortice tenui fere nigro. Folia opposita subsessilia late elliptica acuminata basi acuta 20–25 cm. longa 7–9 cm. lata glabra subcoriacea subtus sine domatiis. Inflorescentia terminalis umbelliformis pauciflora, pedunculo ca. 0.5 cm. longo, bracteis scariaceis minimis. Flores speciosissimi albi; pedicellis gracillimis ca. 2.5 cm. longis; calycis laciniis aequalibus plus-minus imbricatis ovato-trigonalibus acutis 0.4 cm. longis scariaceis papillatis intus cum squamellis alternatis solitariis bifidis; corolla infundibuliformi extus glabra vel indistincte papillata, tubo proprio valde arcuato ca. 3.5 cm. longo basi ca. 0.3 cm. diam. apicem versus sensim attentuato, faucibus conicis ca. 1.5 cm. longis ostio ca. 1 cm. diam., limbi lobis oblique ovatis late acutis ca. 2 cm. longis basi 1.5 cm. latis paulo patulis; ovariis late oblongoideis ca. 0.2 cm. longis dense puberulo-papillatis cum nectariis 5 compressis ca. 0.7 cm. longis, stylo gracili ca. 1.2 cm. longo, stigmate oblongo-fusiformi ca. 0.2 cm. longi; antheris anguste lanceo-

lato-sagittatis paene inclusis ca. 0.6 cm. longis dorso apicem versus sparse pilosulis. Fructus ignoti.—VENEZUELA: AMAZONAS: Maroa, Río Guainía, alt. 127 m., Feb. 10, 1942, *L. Williams 14237*, in Herb. Missouri Bot. Garden, HOLOTYPE.

For a *Malouetia*, this species is almost alarming, with its relatively gigantic, infundibuliform corollas so alien to its cogeners. Surely it will be made the type of a distinct subgenus by the next monographer of the genus. I am persuaded to forbear the erection of a new genus because the affinities of *M. grandiflora* so obviously are with *Malouetia*, as seen in the habit of the plants, the rather distinctive bark, the leaves (although our specimen is without the domatia found with more or less regularity in the other species), and the structure of the inflorescence and reproductive organs.

Explanation of Plate

PLATE 40

Habit and floral dissections of *Secondatia Adolphii* Azumbuja.

AZUMBUJA & WOODSON—NEW APOCYNACEAE

Explanation of Plate

PLATE 41

Fruit and seed of *Secondatia Adolphii* Azumbuja.

foto JOÃO BARBOSA
10 cm.

GENERAL INDEX TO VOLUME XXXVI

New scientific names of plants and the final members of new combinations are printed in **bold-face** type; synonyms and page numbers having reference to figures and plates, in *italics;* and all other matter in ordinary type.

A

Adenodiscus, 511; *mexicanus*, 523
Allen, P. H. Orchidaceae of Panama (third part), 1; (fourth part), 133
Ancash, On some uses of maize in the Sierra of, 405
Anderson, Edgar: Charles M. Rick and. On some uses of maize in the Sierra of Ancash, 405; Stoner, C. R., and. Maize among the Hill Peoples of Assam, 355
Andrews, Henry N., Jr. Nucellangium, a new genus of fossil seeds previously assigned to Lepidocarpon, 479
Aneurophyton, 291
Apocynaceae of South America, New, 543
Asia: maize in, 389; distribution of major races in, 391
Assam, Maize among the Hill Peoples of, 355
Assam hills: economics in the, 375; history in the, 374; map of, *357;* tribes of, 356; varieties of maize among the, 359
Azumbuja, David de, and Robert E. Woodson, Jr. New Apocynaceae of South America, 543

B

Baxter, Robert W. Some Pteridosperm stems and fructifications with particular reference to the Medullosae, 287
Beer prepared from maize: in Assam, 377, in Peru, 410
Bhutan, maize in, 372
Burma, maize in, 373

C

Calamopitys, 291
California, Assamese varieties of maize grown in, 356, 379
Callejon de Huailas, uses of maize in the, 406
Cancha, preparation of, from maize, 409
Carboniferous plants, 287, 479
Cardiocarpus, 492; bicuspidatus, 493; injens, 492; minor, 492
Chicha, preparation of, from maize, 410; chicha de jora, 410; chicha morada, 411
Chochaca, preparation of, from maize, 411
Chondrorhyncha **aromatica**, 85; **caloglossa**, 85; **costaricensis**, 86; **discolor**, 87; **marginata**, 88, *89*
Chromosomes in Paphiopedilum: comparative length of, in P. Lawrenceanum and P. callosum, *441*, *443;* numbers of, 445; terminal, 453, *468*
Coal balls, fossils found in, 287, 479
Coix, uses of, by the Assamese tribes, 358
Cordaianthus spicatus, 493
Cusqueño blanco, 406
Cypripedilum, 433
Cypripedium, 433; *callosum*, 434; *Hyeanum*, 435; *Lawrenceanum* var. *Hyeanum*, 435
Cytology: of Paphiopedilum callosum, 447; of P. Maudiae Hort., 433, 449; of P. Lawrenceanum, 448; analysis of root-tips, 440; of yeasts, 260

D

Dafla tribe of Assam, maize culture by the, 368, *398*
Darrah, W. H., description of coal-ball fossil by, 479
Dolerotheca, 315; formosa, 316, *344*, *348;* Reedana, 317; **Schopfii**, 317, *348*, *350*, *352;* **sclerotica**, 315, *316*, *346*, *348*, *352;* villosa, 317

E

Economics in the Assam hills, 375
Euspermopteris, 294
Ethnology in relation to maize, 355, 405

F

Ferns, fossil, 287
Food plants among the Hill Peoples of Assam, 374
Fossil: fructifications, 315; seeds, 479; stems, 287

G

Galactose, fermentation of, 260, 265
Grewia terebinthinaceus, 513

H

Heliocarpus, A revision of the genus, 507; generic relationships, 507; economic value of, 509; geographic distribution, 509; taxonomy, 511; vernacular names, 510
Heliocarpus, 511; americanus, 528, 532; *americanus* var. *popayanensis*, 532, var. *typica*, 528; appendiculatus, 526; attenuatus, 520; *australis*, 532; *belizensis*, 523; *boliviensis*, 532; *costaricensis*, 523; *Caecaliae*, 530; *chontalensis*, 526; *cuspidatus*, 530; *diclinus*, 532; Donnell-Smithii, 530; *excelsior*, 536; *floribundus*, 530; *Gentlei*, 536; *glaber*, 517; *glabrescens*, 523; *glanduliferus*, 523; *horridus*, 530; *laevis*, 521; mexicanus, 523; *microcarpus*, 513; *Nelsoni*, 513; nodiflorus, 536; occidentalis, 521; pallidus, 515; Palmeri, 517; *polyandrus*, 517, var. *nodiflorus*, 536; popayanensis, 532; *popayanensis* var. *grandifolius*, 532, var. *Schumanni*, 532, var. *trichopoda*, 532; *reticulatus*, 513; *Rosei*, 532; *rudis*, 532; *stipulatus*, 532; *subtrilobus*, 532; terebinthinaceus, 513; *tomentosus*, 528; *trichopodus*, 532; *velutinus*, 515; *viridis*, 520; *yucatanensis*, 523
Hermann, Frederick J. New species of Lonchocarpus from Panama, 281
Heterangium Grievii, 204; Kukuki, 294; minimum, 294
Hybrids: of Paphiopedilum, 433; of Saccharomyces, 259

I

Inheritance in yeast, 260
Internode diagram of a variety of Assamese maize, *381*
Iowa, fossils found in coal-balls from, 287, 479

J

Job's tears, use of, by the Assamese tribes, 358

K

Kaloxylon, 293

L

Lacmellea **speciosa**, 543
Lay, Ko Ko. A revision of the genus Heliocarpus L., 507
Lepidocarpon, 486; glabrum, 479, 491; lomaxi, 486
Lonchocarpus, New species of, from Panama, 281
Lonchocarpus atropurpureus, 282; **calcaratus**, 282; densiflorus, 284; glabrescens, 284; **oliganthus**, 281; parviflorus, 282; praecox, 284
Lyginopteris, 290

M

McQuade, Henry A. Cytology of Paphiopedilium Maudiae Hort., 433
Maíz dulce, 409; maíz morada, 411
Maize: among the Hill Peoples of Assam, 355, culture of, 376; geographic distribution of, 405; history of, 405; in hill areas outside Assam, 372; in the Orient, 355; morphological survey of, grown by the Nagas, 379; On some uses of, in the Sierra of Ancash, 405; races of, in South America and Asia, 390; uses of, in Assam, 377, in Peru, 405; varieties of, 380, 383
Maize: "Caribbean", 383; "Drooping Waxy", 381, 386, *402*; "Early Slender", 383, *400*; "Early Upright", 384, *404*; "Late Sidewise", *381*, 385, *402*; "Late Upright", 383, 384, *404*.
Malouetia cestroides, 544; **grandiflora**, 544; **parviflora**, 544
Manioc, culture of, in the Assam Hills, 374
Manipur State: maize in, 373; tribes of, 357
Marsilea, 492
Medicine, use of corn preparations in, 409
Medullosa, 290; anglica, var. ioensis, 298; centrofilis, 298; distelica, 298; **elongata**, 301; **endocentrica**, 303; Leuckarti, 298; Noei, 298; **primaeva**, 298; Thompsonii, 298
Medullosae, Some Pteridosperm stems and fructifications with particular reference to the, 287
Melibiose, fermentation of, 260, 265
Mendelian, Non-, segregations in Saccharomyces, 259
Microspermopteris aphyllum, 289, *322*, *324*; partial reconstruction of, *382*
Millet, use of, by the Assamese tribes, 358
Monba tribe of Assam, 358, *396*; threshing maize, *396*; maize stacked for ripening, *396*
Mote, preparation of, from maize, 411
Mundkur, Balaji D. Evidence excluding mutations, polysomy, and polyploidy as possible causes of non-Mendelian inheritance in Saccharomyces, 259

N

Naga tribes of Assam, 357, 359, *398*; corner of a "jhum" field, *398*; varieties of maize

grown by, 379, characteristics of, 384
Nepal, maize in, 373
Non-Mendelian segregations in Saccharomyces, Evidence as possible causes of, 259
Nucellus, fossil, 480, 486
Nucellangium, a new genus of fossil seeds previously assigned to Lepidocarpon, 479
Nucellangium glabrum, 491

O

Olla canchera, a prehistoric vessel used to parch maize, 409, *409*
Orient, maize in the, 355
Orchidaceae: of Panama (third part), 1, (fourth part), 133; Index (part III), 247; Pfitzer's key to Pleonandrae of, 434; Rolfe's key to suborder Diandrae of, 434

P

Paleobotany studies, 287
Panama: Flora of, Part III, Fascicle 4 (Orchidaceae, third part), 1, Fascicle 5 (Orchidaceae, fourth part), 133, Index to Part III, 247; New species of Lonchocarpus from, 281; A first record of the genus Qualea in, 285
Paphiopedilum Maudiae Hort., The cytology of, 433
Paphiopedilum, 433; albino forms of, 437; chromosome numbers in, 445; cytology of P. callosum, 447, of P. Lawrenceanum, 448, of P. Maudiae, 449; key to subgenera, 435; meiosis in, 447; root-tips, 440; taxonomy of, 433
Paphiopedilum: "Alma Gavaert", 438; bellatulum, var. album, 437; callosum, 434, 437, 441, 447, *466*, list of crosses in which used as parent, 459, var. Sanderae, 433, 434, 437, 459; Charlesworthii var. album, 437; Curtisii, 437; "Emerald", 438; "Enchantress", 438; Holdenii, 438; insigne var. Sanderae, 438, var. Sanderianum, 438; Lawrenceanum, 435, 437, 448, *466*, list of crosses in which used as parent, 462, var. Hyeanum, 433, 435, 437; Maudiae, 433, 435, analysis of, 448, list of crosses in which used as parent, 456, var. "Bank House", 436, var. "Dell", 436, var. magnificum, 436, *466*, var. "Westonbirt", 436; niveum, 437; Rosettii, 438; "Warden", 438
Paphiopedium, 433
Peru, uses of maize in Ancash, Dept. of, 405
Psilophyton princeps, 295
Photographing spores of Selaginella, 414
Phragmopedilum, 433
Phragmopedium, 433
Phytolaccaceae, 475
Pollen grains: of Paphiopedilum callosum, 447, *470;* of P. Lawrenceanum, 449, *470;* of P. Maudiae, 450, *470*
Polynesians, transfer of crops by, 292
Popcorns: in Assam, 379; Oriental, 355; in Peru, 409
Potato, culture of, in the Assam Hills, 374
Pteridosperm stems and fructifications, Some, with particular reference to the Medullosae, 287

Q

Qualea, A first record for the genus (Vochysiaceae), in North America, 285
Qualea **cymulosa**, 285; rupicola, 286

R

Rhetinangium, 290
Rice in the Assam Hills, 358
Rick, Charles M., and Edgar Anderson. On some uses of maize in the Sierra of Ancash, 405
Rogers, David J. Stegnosperma: A new species and a generic commentary, 475

S

Saccharomyces: Evidence excluding mutations, polysomy and polyploidy as possible causes of non-Mendelian inheritance in, 259; tetrad analyses of crosses of, 260
Schery, Robert W.: A first record for the genus Qualea (Vochysiaceae) from North America (Panama), 285; Robert E. Woodson, Jr., and collaborators. Flora of Panama, Part III, Fasc. 4, 1, Fasc. 5, 133
Schopfiastrum, 291
Secondatia **Adolphii**, 543, *546*, *548;* Duckei, 543
Seed-ferns, 288; comparative characters of stem genera of, 290
Seeds, fossil, 479, "normal", 480, "proliferated", 486
Segregations in yeast, Non-Mendelian, 259, 271
Selaginella, Spores of the genus, in North America north of Mexico, 413
Selaginella, 413; acanthonota, 419, *426;* apoda, 423, *431;* arenicola, 418, *425;* arizonica, 422, *430;* armata, 413, 414, 422, *431;* asprella, 420, 421, *429;* Bigelovii, 417, 418, *425;* cinerascens, 419, *427;* Ser. Circinatae, 423; Coryi, 418; Ser. Decumbentes, 422; densa, 413, 420, 421, *429;* Douglasii, 422, *431;* eremophila, 422, *430;* subg. Euselaginella, 415, 417;

floridana, 419, *426;* funiformis, 419, *426;* Hanseni, 421, 422, *430;* lepidophylla, 423, *431;* leucobryoides, 420, *428;* mutica, 419, *427;* neomexicana, 418; oregana, 419, *426;* Parishii, 422; pilifera, 413, 423, *431;* Riddellii, 418, *425;* rupestris, 413, 417, 420, 421, *429;* rupincola, 417, 418, *425;* scopulorum, 420, 421, *429;* selaginoides, 413, 414, 415, 417, *424;* Sheldonii, 422, *430; Sherwoodii*, 417, *424;* sibirica, 421, *428;* subg. Stachygynandrum, 416, 422; Standleyi, 420, *428;* tortipila, 414, 417, *424;* Underwoodii, 419, *427;* Wallacei, 413, 421, *428;* Watsoni, 420, *427;* Wrightii, 421, *430*
Selenipedilum, 433
Selenipedium, 433
Sierra of Ancash, uses of maize in, 406
Sikkim, maize in, 372
Sorghum: relation between maize and, 393; use of, by the Assamese tribes, 358
South America, New Apocynaceae of, 543; maize of, 389, 405
Sporangium, fossil, 480, 486
Spores of the genus Selaginella in North America north of Mexico, 413
"Star rings" from carboniferous species of Medullosa, 312, *338*, *340*, *342*
Stegnosperma: A new species and a generic commentary, 475; cubense, 476; *halimifolia*, 477; halimifolium, 475, 477; *halimifolium*, 476; *scandens*, 476; Watsonii, 475
Stem genera of seed-ferns, 290
Stems and fructifications, Some Pteridosperm, with particular reference to the Medullosae, 287
Stenomylon, 291
Stonor, C. R., and Edgar Anderson. Maize among the Hill Peoples of Assam, 355
Sutcliffia, 291

T

Tercio pelo, 409
Tetrad analyses of yeast hybrids, 260, 268
Tiestos, 409
Tocos, preparation of, from maize, 406
Trichilia scandens, 476
Triumfetta, 1; *mexicana*, 523
Tryon, Alice F. Spores of the genus Selaginella in North America north of Mexico, 413

V

Valcárcel's illustration of Olla canchera, 409
Vitamin synthesizing abilities in yeasts, segregations of, 271
Vochysiaceae, the genus Lonchocarpus of the, 285

W

Woodson, Robert E., Jr., and David de Azumbuja. New Apocynaceae of South America, 543; Robert W. Schery and, and collaborators. Flora of Panama, Part III, Fasc. 4, 1, Fasc. 5, 133

Y

Yeast hybrids, tetrad analysis of, 260
Yeast, see Saccharomyces

Z

Zea Mays—see Maize

STAFF
OF THE MISSOURI BOTANICAL GARDEN

Director
GEORGE T. MOORE

HERMANN VON SCHRENK,
Pathologist

ROBERT W. SCHERY,
Research Associate

JESSE M. GREENMAN,
Curator Emeritus of the Herbarium

GUSTAV A. L. MEHLQUIST,
Research Horticulturist

CARROLL W. DODGE,
Mycologist

ROLLA M. TRYON,
Assistant Curator of the Herbarium

EDGAR ANDERSON,
Geneticist

GEORGE B. VAN SCHAACK,
Honorary Curator of Grasses

ROBERT E. WOODSON, JR.
Curator of the Herbarium

JULIAN A. STEYERMARK,
Honorary Research Associate

HENRY N. ANDREWS,
Paleobotanist

NELL C. HORNER,
Librarian and Editor of Publications

GERALD ULRICI,
Business Manager

BOARD OF TRUSTEES
OF THE MISSOURI BOTANICAL GARDEN

President
RICHARD J. LOCKWOOD

Vice-President
DANIEL K. CATLIN

Second Vice-President
EUGENE PETTUS

L. RAY CARTER
DUDLEY FRENCH
HENRY HITCHCOCK
JOHN S. LEHMANN
GEORGE T. MOORE
A. WESSEL SHAPLEIGH
ETHAN A. H. SHEPLEY

***EX-OFFICIO* MEMBERS**

ARTHUR H. COMPTON,
Chancellor of Washington University

WILLIAM P. GRUNER,
President of the Academy of Science of St. Louis

JOSEPH M. DARST,
Mayor of the City of St. Louis

WILLIAM SCARLETT,
Bishop of the Diocese of Missouri

HERBERT C. WINTERER
President of the Board of Education of St. Louis

GERALD ULRICI, *Secretary*